

EAST AFRICAN MAMMALS

An Atlas of Evolution in Africa

Volume IIB

Jonathan Kingdon



This is one part of the second volume in an already widely acclaimed work on the mammals of Kenya, Uganda and Tanzania.

As with its predecessor, this volume (covering the smaller and lesser known mammals) abounds with illustrations and sketches of East African fauna. The quality of the drawings is superb, comprising not only life sketches, but anatomical detail on skeleton and musculature as well. The author's aim however is not only to illustrate the East African fauna, but also to encompass their form and habits, their past and present distributions, and the evolutionary processes that have controlled both genetic speciation and changes in the patterns of their distribution. Thus, each species dealt with in this volume has its own comprehensive survey covering geographical distribution, evolutionary relationships, ecology, behaviour and problems of conservation. The net result of this brilliant work is the synthesis of several disciplines into a unique zoogeographic treatment of mammalian ecology that can ill afford to be ignored by any who claim to have an interest in this field of study.

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**EAST
AFRICAN MAMMALS**

Jonathan Kingdon

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An Atlas of Evolution in Africa

Volume II Part B (Hares and Rodents)



1974



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Hares

LAGOMORPHA

Although once regarded as rodents, the hares are now known to represent a completely separate evolutionary line, the origins of which are unknown.

Sych (1966) has reviewed the various hypotheses on the origin of the Lagomorpha. Early lagomorphs were very different to the modern hares, but they are recognized in the late Palaeocene and are quite numerous as fossils from the Eocene onwards.

Hares and rabbits occur today on all continents but were introduced by man into South America and Australasia. In Australia, hare-wallabies, *Lagorchestes leporides*, seem to have filled the hare niche, but these are now very rare. In South America, where many unique mammal groups evolved in complete isolation, an extraordinary degree of convergence was achieved by the Miocene notoungulate, *Pachyruchos moyani*, which has almost identical body architecture to a hare. Of living South American fauna, the hystricomorph, *Dolichotis*, fills the hare niche.

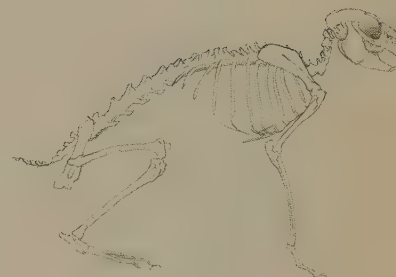
Hares are very successful animals and their ancestors probably evolved first in Eurasia, adapting at an early date to the special requirements of open grassland. They had reached North America by the Oligocene and the first complete skeleton of a lagomorph, *Palaeolagus haydeni*, comes from the North American Oligocene.

LEPORIDAE

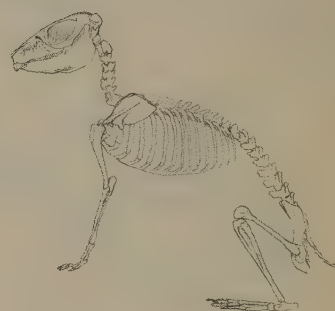
In Africa the first fossils are the Miocene *Australagomys* and *Kenyalagomys*. The family to which modern hares belong, the Leporidae, seems to appear rather late in the fossil record and this family is likely to have evolved from a Eurasian lagomorph ancestor, possibly invading Africa in the late Miocene or early Pliocene. A Lower Pleistocene hare, *Serengetilagus*, is known from Laetoli and *Lepus veter* from the Middle Pleistocene at Kanjera.

In Africa hares are represented by open country forms, *Lepus*, rock jumpers, *Pronolagus*, and an intermediate rocky grassland type, *Poelagus*. Although the skeleton is built on similar lines, the proportions of each form are modified in a way suited to their different habitats, *Lepus* being long-limbed and slender for sustained speed in the open, *Pronolagus* short-legged and more stoutly built, for agility and adroitness in sudden dashes amongst rocks and bushes, while *Poelagus* is somewhat between the two extremes. *Poelagus* is often called the Bunyoro rabbit and it does in fact have some resemblances with the common rabbit *Oryctolagus*. For instance, young *Poelagus* are born in a less developed condition than true hares and are hidden in crevices or short burrows. Could *Poelagus* represent a relic form linking hares and rabbits?

The behaviour of hares has received scant attention in Africa; a neglect that is apparent in the profiles that follow.



Lepus.



Pachyruchos moyani.

KEY

BROWN HARE *Lepus capensis*

Front surfaces of upper incisors in same plane.
One shallow groove without cement.
Muzzle less projecting.
Usually lighter.
Ears often shorter than skull.
Nape greyish buff.
White spot on head rare.

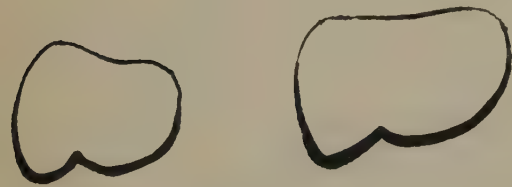
CRAWSHAY'S HARE *Lepus crawshayi*

Front surface of upper incisors form an angle.
Groove or grooves filled with cement.
Muzzle projects more.
Usually darker.
Ears always longer than skull.
Nape rufous.
White spot on head common.

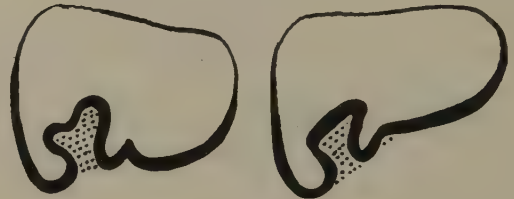
L. crawshayi
Mesopterygoid
space larger

L. whytei
Mesopterygoid
space small

Cross section of incisors of two species of *Lepus*.



L. capensis.



L. crawshayi.

Hare (*Lepus*)

Family Leporidae
Order Lagomorpha

Measurements head and body

400—600 mm (ave. 500)

tail 70—135 mm (ave. 100)

hindfoot 100—124 mm (ave. 120)

ear 78—110 mm (ave. 95)

weight 1.75 (1.1—3) kg

Lepus capensis

head and body

411—480 mm (ave. 450)

tail 73—134 mm (ave. 100)

hindfoot 103—119 mm (ave. 115)

ear 85—114 mm

weight 1—2.5 kg

Lepus crawshayi and *Lepus whytei*

Local names

Sungura (Kiswahili), Chungula
(Kimwera), Munyangaa (Kinyaturu), Uyungula
(Kimakonde), Kululu (Kinyakyusa),
Nduyu (Lubukusu), Sude (Kikinga),
Kami (Kikerewe), Irangut
(Kimasai), Cheprayut (Kisebei),

Shikalla (Tiriki), Akamuyu
(Luganda), Akame (Runyoro,
Runyankole), Apwoyo (Lwo),
Kifoyo (Ragoli), Apoo (Ateso), Ito
(Lugbara), Hiless (Kiliangulu),
Kwilil (Karamojong)

Hare (*Lepus*)

Species

Lepus capensis

Lepus crawshayi

Lepus whytei

Lepus victoriae?



The hare is a familiar animal and needs no description. However the identification of species is by no means as simple. A great deal remains to be learned about hares in East Africa, where at least two and possibly three or four species of the genus *Lepus* occur.

The commonest and most widespread is the brown hare, *Lepus capensis*, which is distributed throughout Africa and Eurasia. The other common species is *L. crawshayi*, which also has an Asian relative, *L. nigricollis* (Petter, 1959, 1961, 1963). Although virtually impossible to tell apart in the field, a combination of average characteristics (listed opposite) serves to distinguish

L. crawshayi.



L. capensis.



L. crawshayi.



L. whytei.

each species, although no one characteristic alone is decisive.

To be so widely represented in both Eurasia and Africa the two species presumably differentiated at an early date. In Africa *L. capensis* is commonest in the more open and more arid habitats, *L. crawshayi* in somewhat moister and more wooded savannas, notwithstanding this the two species are sympatric over very large areas. The third species, *L. whytei*, may be closely related to *L. crawshayi*. *Lepus victoriae* is a large drab coloured hare of uncertain affinities, but it may be a race of *capensis*.

The following account is derived almost entirely from observations of *L. capensis*, both in Africa and also in Europe, where it is a very familiar animal and the object of beagling and coursing with dogs. A whole vocabulary of old English terms surrounds hares: the greyhounds are "slipped" after a "jack" or a "jill"; the hares may use "pads" (paths) or "smeuses" (habitual passageways through hedges), seeking their "form" (resting place), in which might be found a "kindle" of "leverets"; when chased by the beagles, hares are apt to make a "wrench" (a right-angled turn made at great speed).

Their food is mostly grass and herbs but they also gnaw at exposed roots, bark, shoots, the pulp of fallen fruits, berries and they occasionally pluck leaves or eat fungi. Favourite foods seem to be the plants of the daisy family, Compositae. Herbaceous vegetation is grazed directly, while twigs and larger items are held steady with the forepaws. Like all lagomorphs, they circulate food twice, producing soft caecotroph pellets during the night and dry dung pellets by day.

Stewart (1971) has made a comparative study of the food preferences of *capensis* and *crawshayi* in the Kenya Rift Valley. His study showed significant differences. *L. capensis* ate more herbs and *Themeda* grass than *L. crawshayi*, and more silica particles in the faeces suggested that *L. capensis* grazes closer to the ground. The table opposite summarizes the more important differences in diet between the two species.

When a hare is approached, it relies on its camouflage to the last moment, crouching lower and lower and apparently drawing its fur tighter and tighter to its body as the enemy draws nearer. Leverets are very tight sitters and depend on this for survival. Robson (1961) tells of two young hares being tethered outside a house so that their mother could suckle them. In spite of an eagle owl using the verandah regularly and the presence of numerous carnivores, one young survived a week before it was taken, presumably by the eagle owl. In the circumstances it is surprising that they were not taken on the first night. They must also rely on carrying very little scent when young. When pursued by dogs, African hares have often been seen to take refuge in aardvark holes or warthog burrows.

Populations of hares in Europe have been shown to be subject to fluctuations (Middleton, 1934). I believe that similar increases and decreases in hare numbers occur in Africa. In parts of Tanzania hares are sighted very much more frequently along the roads at night during some years, and much less frequently in other years.

The hare breeds throughout the year in East Africa but there is an increase in weight in the rains and, in Kenya, litters increase in numbers from an average of one young to two between September and January (Flux, 1969). Gestation is in the region of six weeks. Kolosov (1941) has shown that hares

SIGNIFICANT DIFFERENCES IN MEAN PROPORTIONS
OF DIFFERENT PLANT ITEMS IN THE FAECES OF
TWO *LEPUS* SPECIES FROM THE SAME HABITAT
(FROM STEWART, 1971)

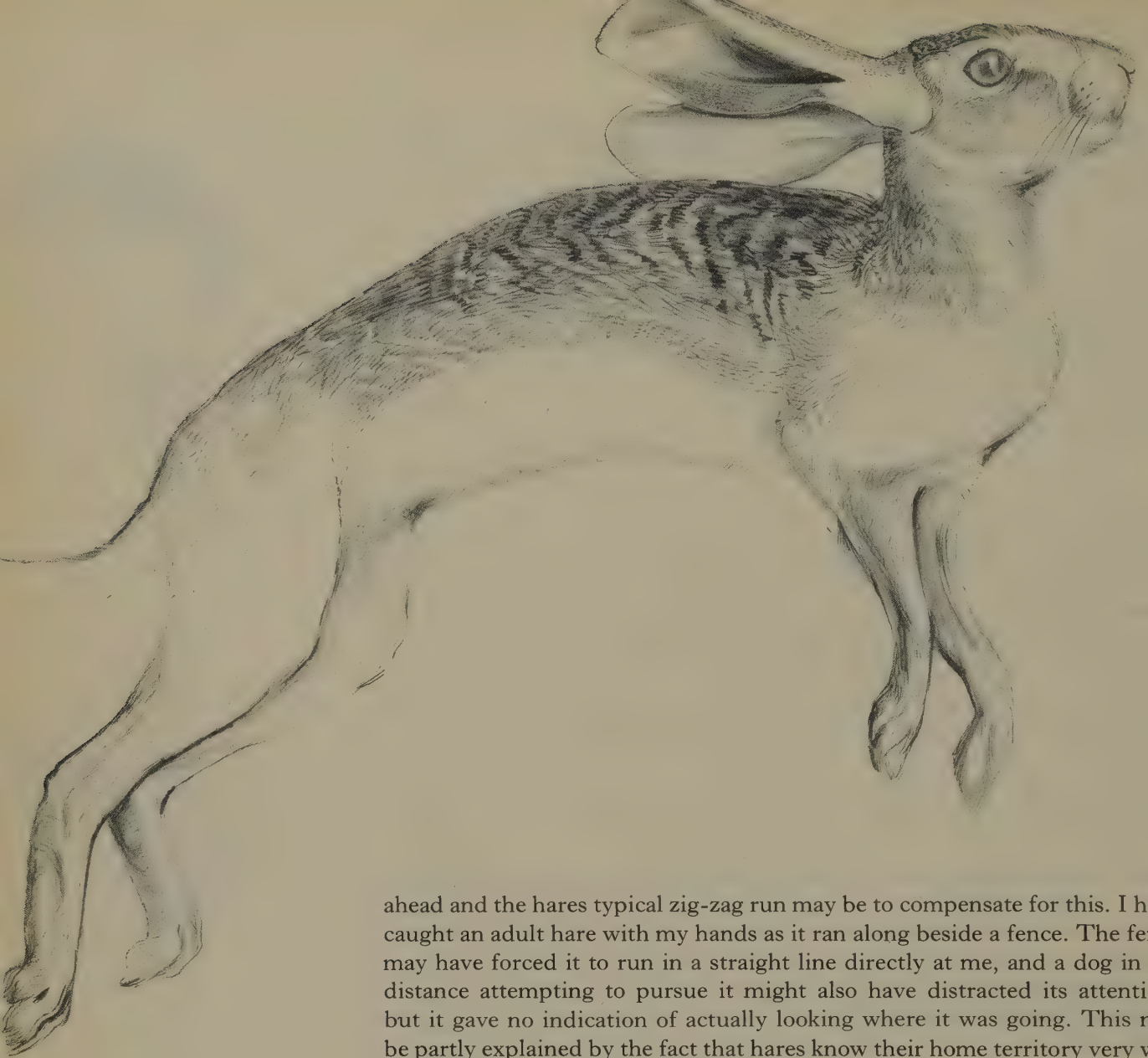
Plant item	<i>capensis</i>	<i>crawshayi</i>
<i>Digitaria</i> spp.	8.6%	18.0%
<i>Hyparrhenia</i> spp.	0.2%	10.7%
<i>Themeda triandra</i>	3.6%	0.8%
dicotyledons	6.3%	1.4%
grass sheath and/or stem epidermis	34.4%	23%

readily reabsorb embryos and in the Caucasus there is a 25% intrauterine loss in Autumn. As many as four litters have been recorded in one year in Germany. Courtship and the associated rivalry of males draw the solitary hares together and, at this time, groups will chase one another, one loping after the other and as many as seven males may pursue a female.

Fights are common, even between the sexes, but only the males seem to fight in earnest and will even occasionally kill one another. Fighting consists of rearing up and boxing with the forelegs, meanwhile wheeling round and round. When females fight with males, this seems to act as a stimulus to sexual behaviour. Harris (1970) watched a pair, boxing, chasing, feeding and lying still in between copulation. They copulated at least seven times in about 2½ hours. The couple pay attention to genitalia and also to the face and ears, which they repeatedly lick and nuzzle. The orange neck patch becomes a special focus for the male's attention whilst copulating and he may nibble and pull hair out. Sometimes females suffer wounds, as hares are very easily damaged. The skin tears and their skulls easily crack on impact if they fall.

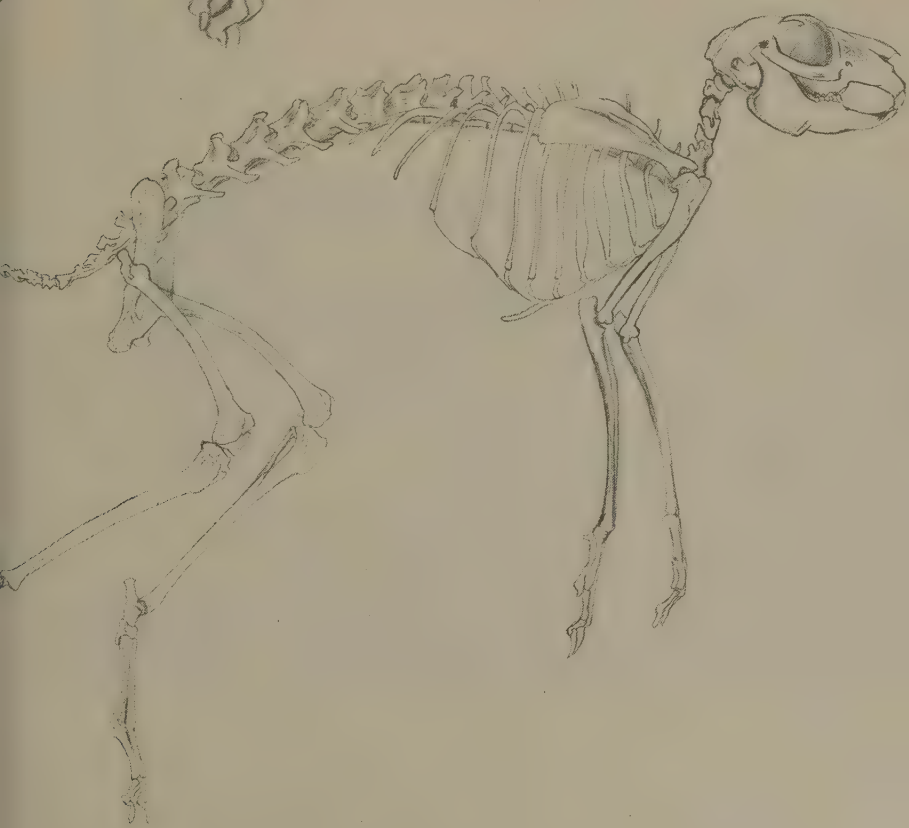
The young are born fully haired and with open eyes and as many as seven young have been recorded, although one or two are the usual number in East Africa. The young may be together initially, but the mother often separates them and visits them in turn to suckle. She may bleat to her young but usually approaches very circumspectly and has been reported to make a prodigious leap in and out of the leverets' forms. When discovered, infant hares sometimes try to box, bite or make toad-like leaps and can growl and grind their teeth. They are weaned and independent at the age of one month and are sexually mature at eight months. The young are playful and pet hares enjoy being chased and then become the pursuers themselves. Webb's hare would play at chasing an apple that it rolled over the floor with its paws.

Hares have very good sight, hearing and sense of smell. They often rise on their hind legs in long grass to get a more elevated view and they must rely on sight to escape enemies, particularly hawks and owls. Their own cryptic colouring is difficult to see but the ear is very distinctly marked and the hare, no less than the experienced naturalist or hunter, must be adept at picking out the white ear margin and black tip. The ears are a very important signalling device and their positions change with moods, as well as being responsive to the direction of sounds. The eyes are not well placed for vision immediately



ahead and the hares typical zig-zag run may be to compensate for this. I have caught an adult hare with my hands as it ran along beside a fence. The fence may have forced it to run in a straight line directly at me, and a dog in the distance attempting to pursue it might also have distracted its attention; but it gave no indication of actually looking where it was going. This may be partly explained by the fact that hares know their home territory very well and rely on running over well-worn trails.

The balance of the limbs is such that hares do not attempt to run directly down a steep hill, but always try to follow a gently sloping contour. The feeding or walking gait of a hare is a slow and greatly contracted version of their running gait, with the fore and hind legs moving in pairs. Hares caught in traps tend to be held by both legs at once. Hares can run at speeds exceeding 70 km per hour. They are capable of incredibly sudden turns or wrenches when running at high speed and they also leap sideways, which appears to be part of a built-in defence mechanism, serving to break the scent trail; this behaviour appears in the play of very young hares. They run with their ears erect, but sometimes seem to make a "flat" run with the ears down which must be designed to make them less conspicuous; this posture is also adopted in tangled vegetation, where ears would otherwise get torn. They crouch when resting but are said to sit upright in rain to allow the drips to fall off. A brown hare has been seen to climb into the fork of a tree in Europe, but this must be quite aberrant behaviour. Drumming with the forelegs is a very





common activity with hares and it seems to have a variety of meanings. It has been noticed in situations where it might be interpreted as a warning. A pet hare drummed on a cat's back in retaliation for a clout, and the victor of a mortal fight between male hares drummed on the body of the vanquished.

Cowper, who kept hares in the eighteenth century, described his pet drumming to attract attention:

"He would invite me to the garden by drumming upon my knee, and by a look of such expression as it was not possible to misinterpret. If this rhetoric did not immediately succeed, he would take the skirt of my coat between his teeth and pull at it with all his force."

Cowper kept his hares for nine and twelve years.

Another non-vocal noise made by hares is tooth-grinding, an inconspicuous vibration which could perhaps travel well and serve as a warning signal. Female hares have been reported to make a bleating or "bugling" call to their young and both sexes make low grunts and growls on occasion. They scream very loudly when caught or wounded. Friendly encounters between hares involve much licking and nibbling of hair round the face and ears, where the emphatic markings give scope for expression. Cowper described each of his hares as having a distinct individuality,

"their countenances were so expressive of that character that, when I looked on the face of either, I immediately knew which it was and I am persuaded that among a thousand of them no two could be found exactly similar; a circumstance little suspected by those who have not had opportunity to observe it".

His epitaph on a Hare describes the daily activity of Tiney, "surliest of its kind".

A Turkey carpet was his lawn
Whereon he lov'd to bound
To skip and gambol like a fawn,
And swing his rump around.

His frisking was at ev'ning hours,
For then he lost his fear;
But most before approaching show'rs,
Or when a storm drew near.

Eight years and five round-rolling moons
He thus saw steal away,
Dozing out all his idle noons
And ev'ry night at play.



Judging from various young hares that I have kept and from very numerous encounters in the wild, hares are active for most of the night in fine weather and lie up for the daylight hours. I once encountered a hare that had been lying close beside me for some time on the edge of a thicketed ant hill and it only bestirred itself when I tried to put a butterfly net over it. Long spells of diurnal inaction are typical of hares.

Hares are normally solitary but the mating season can draw numbers of hares together. In Europe, where there is a limited breeding season, there are sometimes aggregations of as many as thirty hares in a small area.

Rothschild (1958) found a peak density of one hare per hectare in a part of France where they were abundant. Country is shared by several hares, and an individual ranges over an area of about 20 sq km. In Europe, the practice of

beagling has revealed that the hare is very reluctant to leave his home range, and will resort to various stratagems such as doubling back and going through streams to remain in the area it knows well. Once forced to leave the home range, it may then flee in a straight line for distances up to 10 km. A brown hare's home range is known by the animal's repeated passage from point to point along established pathways, which are not usually easily visible. The animal possesses several forms and even captives tend to have more than one resting place. The role of scent, which is so difficult to assess, is well illustrated by Cowper:

"These creatures have singular sagacity in discovering the minutest alteration that is made in the place to which they are accustomed and instantly apply their nose to the examination of a new object. A small hole being burnt in the carpet, it was mended with a patch, and that patch in a moment underwent the strictest scrutiny. They seem to be very much directed by the smell in the choice of their favourites: to some persons, though they saw them daily, they could never be reconciled, and would even scream when they attempted to touch them; but a miller coming in engaged their affections at once; his powdered coat had charms that were irresistible."

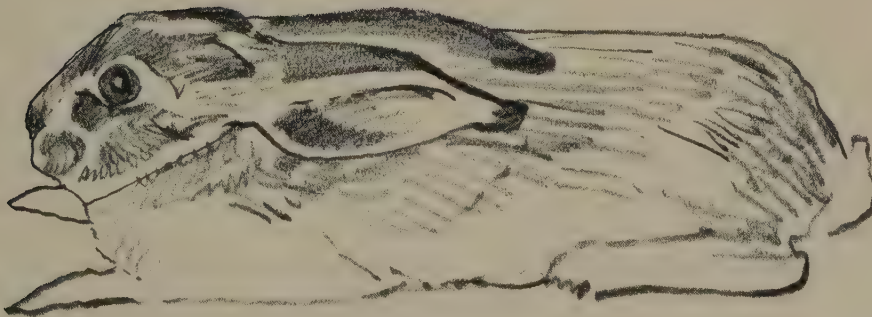
Cowper's keen observation and affection for his hares has been shared by all who have kept them. Cecil Webb, a director of London Zoo, wrote a charming account of a captive blue hare, *L. timidus*.

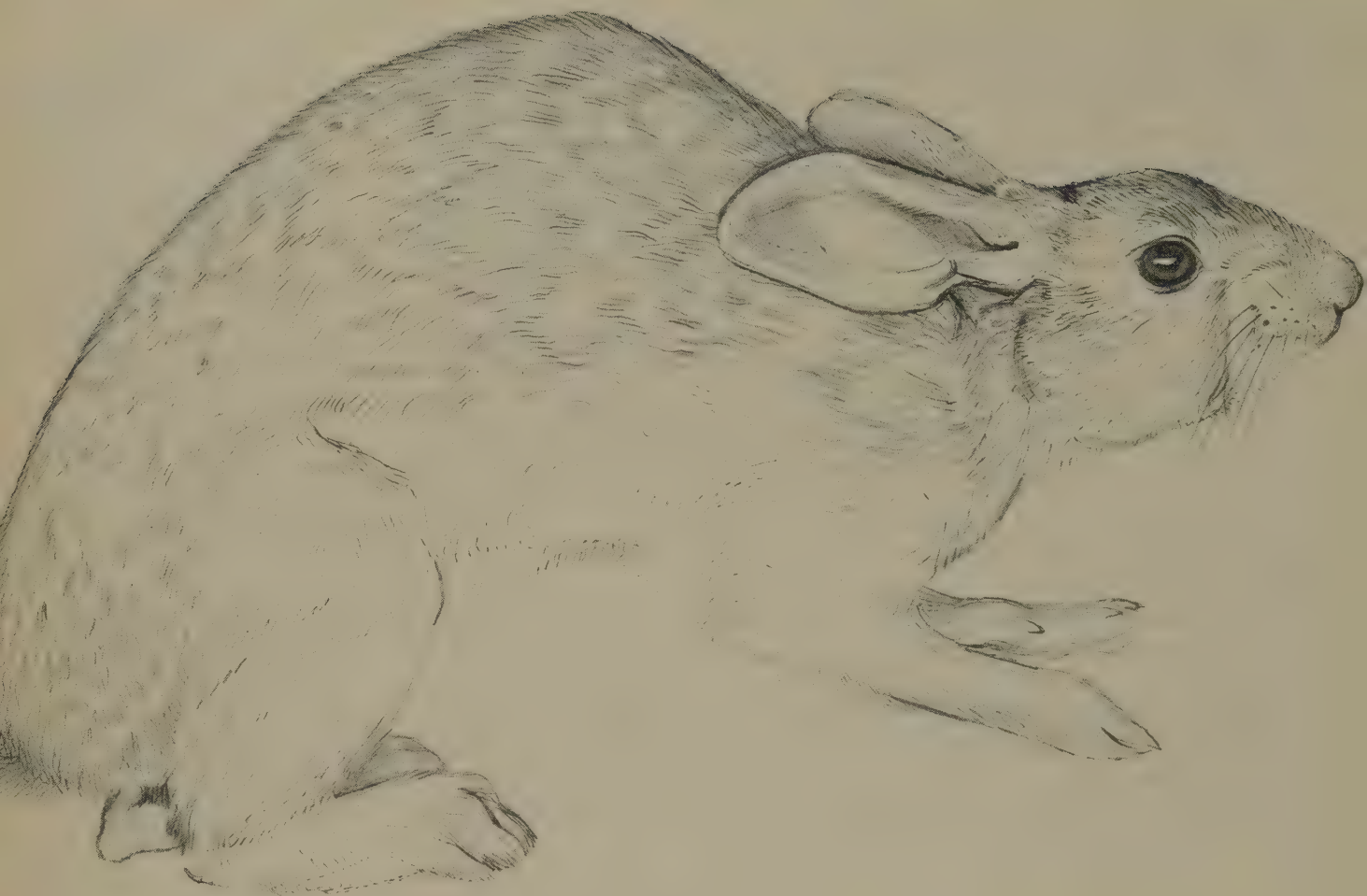
Where they are very numerous they can be a nuisance to agriculture, damaging young wheat and other growing crops, but they are generally hunted for the sake of their meat and the excitement of the chase, rather than as a control measure.

Other predators are hawks, eagles, owls, snakes and many carnivores, baboons have also been seen to catch and kill them.



Young hare.





**Uganda Grass-hare,
Bunyoro Rabbit**
(*Poelagus marjorita*)

Family Leporidae
Order Lagomorpha
Local names
Ebuwa (Lugbara),
Anyadu (Karamojong)

Measurements
head and body

440—500 mm

tail

45—50 mm

hindfoot

90—100 mm

ear

60—65 mm

weight

2—3 kg

Uganda Grass-hare, Bunyoro Rabbit (*Poelagus marjorita*)

The Uganda grass-hare is a short-legged, short-eared hare, which so much resembles a rabbit that experienced naturalists assumed that the animals they saw were feral rabbits. Hale Carpenter mentioned them in 1925 and suggested that they were the descendants of rabbits said to have been imported and released at Masindi in 1881 by Emin Pasha. The first specimens were collected by Lang and Chapin in the North-east Congo in 1912, but were not examined for 25 years, by which time C. Pitman of the Uganda Game Department had collected a series and the animal was described by St Leger in 1929.

Subsequently another race has been described from the Congo and a third from near the Uganda-Sudan border, *P. m. oweni*. It now appears that this hare is quite widespread, having been found as far west as Oubangui and Angola in recent years, and there can be little doubt that it will turn up in new localities further west.

Being nocturnal and fond of rocky eroded situations, it is as easily overlooked as the red rock hare and, along the walls of the western Rift above Lake Albert, *Poelagus* occupies rather similar country to *Pronolagus*. It is, however, more of a rock and grass country animal and favours grassy hills with eroded gullies and thicket or even forest nearby. I have never found a burrow but have put one up in daylight from a form on a rock-strewn hillside and I have found them closely associated with *Hyrax* and possibly they share natural crevices in the rocks for shelter. Karamojong informants who know the animal well state that they often rest up in rocky caves and under bushes where they scrape a small nest (I. Ross, personal communication).

I have once encountered a grass-hare deep in forest, in rather peculiar circumstances. The animal was accompanying a small herd of buffaloes and was very determinedly keeping close to their legs. The buffaloes had very probably come in recently from savanna but it was not possible to know how long they had been in the forest, nor how long the hare had been with them. When the buffaloes took fright, the hare ran with them, and it seemed obvious this was to keep up with them rather than from fright, for it appeared to be unaware of my presence.

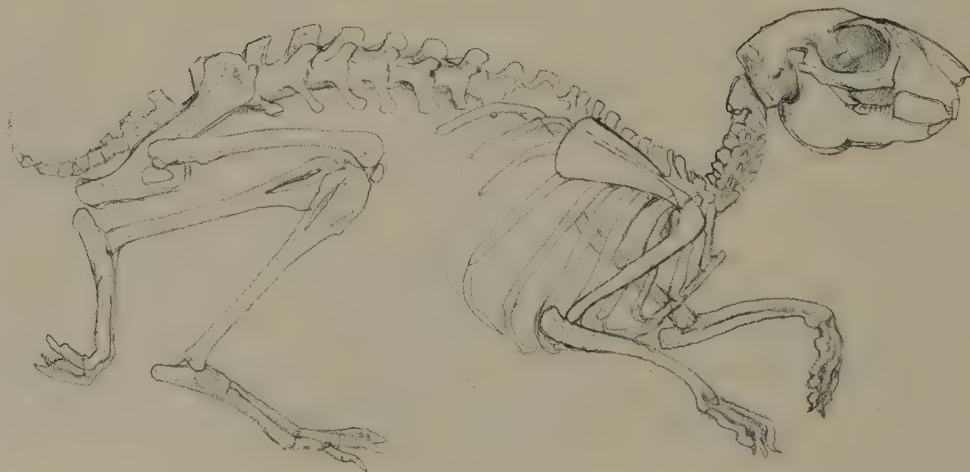
They live in a habitat that is burnt annually and sometimes bi-annually, stripping away their cover and making them much more vulnerable. On the other hand, they are fond of eating flowering heads and growing shoots in short-grass areas so that the early rains are probably a period of optimum feeding and at the same time of maximum risk. During the rainy season, their habitat is heavily overgrown and their passageways at the base of the long grass and scrub are often indistinguishable from those used by numerous other mammals (cane rats, hyrax, etc.) that must move along tunnel-like passages through the tall grass. At this time the grass-hares may seek out heavily grazed patches and the mown verges of roads. The association with buffaloes mentioned earlier might be of great advantage to the hares and the

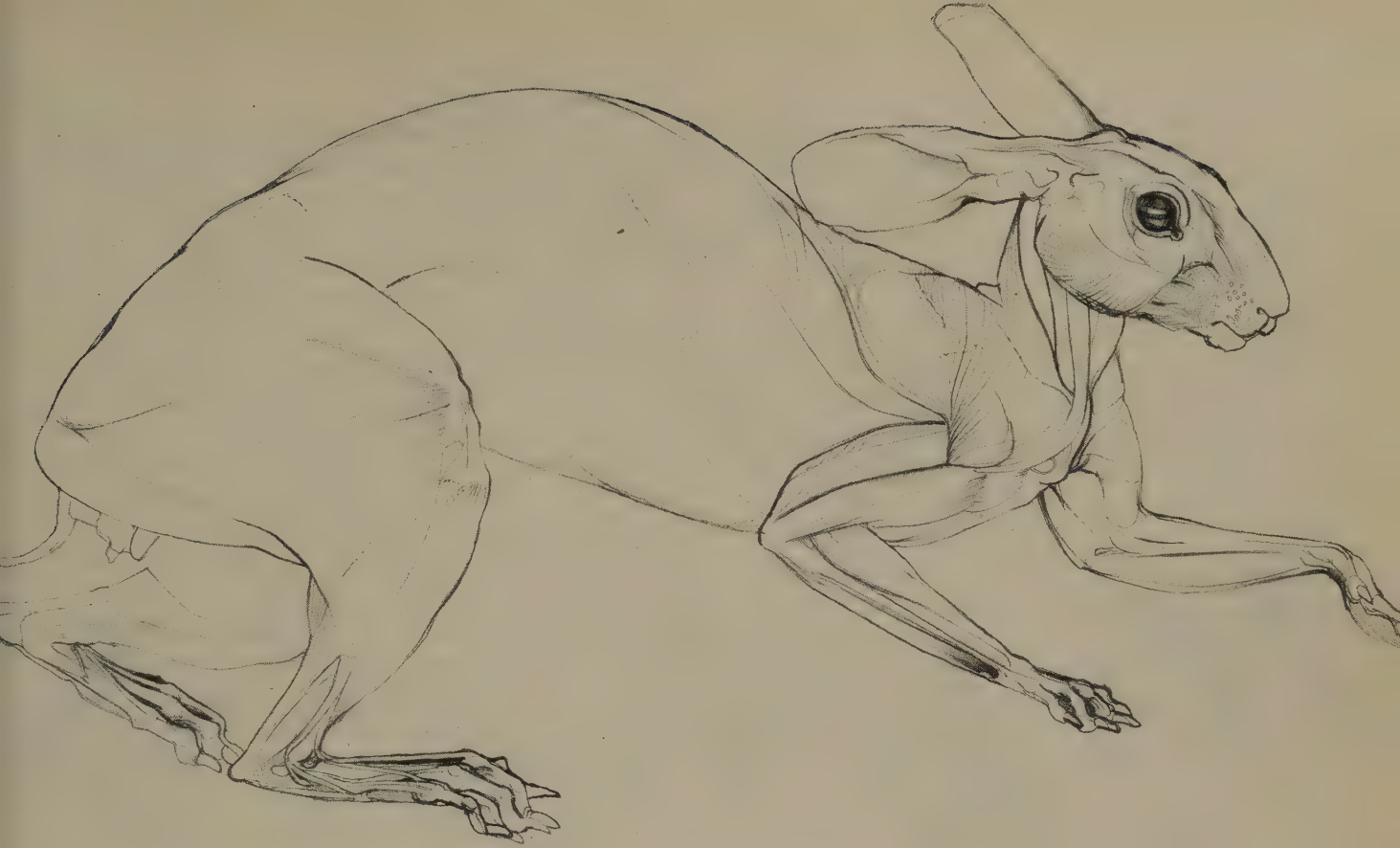




observation might not be as freakish as it appears. Buffaloes are the principal animals maintaining short-grass grazing meadows; these meadows are favoured by the grass-hare and the two animals would tend to feed there at much the same time, so that the hares would benefit from the protection of the buffaloes at a time when they were most vulnerable.

The grass-hares' gait is very much like that of a rabbit and they show the white scut when running in alarm. I have not heard them make any call but they grind their teeth when disturbed in long grass. A torch shone on them at night often gives rise to mild curiosity and one half-grown hare once came up to investigate. In daylight a disturbed hare races for cover.





They feed at night in small groups; casual collecting suggests that these groups consist of pairs, or females with young, or both. They are particularly numerous in several localities in Bunyoro and can generally be found again and again within a small area.

Their predators are numerous; serval cats are particularly common in their habitat as well as genets, *Genetta tigrina* and *G. servalina*. Baboons have been seen to eat *Lepus capensis* at Ishasha (Rowell, 1966) and catch hyraxes in other places; they patrol their habitat and are probably important predators of young grass-hares. Owls and hawks must also take their toll. I have found a juvenile that had been swallowed and then regurgitated by a python. This rejection of what would seem to be an uncomplicated meal is a puzzle. Could the peculiar texture of the coat be a deterrent?

Grass-hares do not at present pose any threat to human activities but they are unlikely to survive in areas where intensive agriculture moves into their habitat.

Their gestation is thought to be about 5 weeks. I have twice collected females that were both pregnant and lactating. In one instance, in May, I also collected the young one who was half the mother's weight—1,240 g to her 2,460 g—and was clearly still suckling as well as feeding on grass. The enormous bladder of this young animal was distended with urine, something I have not noticed in adults.

Some breeding is probably going on throughout the year. Hatt (1940)





reports a pregnant female in August, the same month in which I have collected a pregnant female with young. Hopkins saw half-grown young in late December and I have collected a male with large testes in company with what I took to be a female, in mid-June. Three very young animals in the British Museum collection were found in January and March and A. C. Brooks has also collected a lactating female in late March.

The genitalia are peculiar. The opening in both sexes is flanked on either side by deep glandular pits with large pores on the anterior swollen side of the pocket. The testes lie immediately in front of these pockets and their position is marked by round powder-puff tufts of hair which are also found in the same place in the female. When the penis is retracted the genitalia of both sexes look almost identical.

The young, which number one or two, are born with sparse hair but are blind and helpless; the ears are black and very short. The offspring are born in a short burrow. Major Larken, collector of a new-born infant, now in the British Museum collection, described it as being "accidentally dug out of its *stop* where its mother had concealed it". The breeding burrow is reported by the Karamojong to be concealed with grass and soil. The drawing below represents an 80-mm foetus collected in May and the sketch of a half-grown young shows the more slender build and softer fur of young animals (p. 354).



Genital region of *Poelagus* showing vulv
anus (hairy) and tail.





Red Rock Hare
(*Pronolagus rupestris*)

Family Leporidae
Order Lagomorpha
Local names

Tisi (Kiramba), Mpumbulu
(Kinyamwezi), Ntju (Kirangi)

Measurements
head and body

350—495 mm

tail

40—75 mm

hindfoot

75—100 mm

ear

60—100 mm

weight

2—2.5 kg

Red Rock Hare (*Pronolagus rupestris*)

Race

Pronolagus rupestris vallicola

The red rock hare has a warm grizzled brown back, grey ears and face and rich russet limbs and tail. The under fur is as soft as down and graduates from white to tawny, with thicker hair on the surface of the back. The grizzled effect is due to the dark brown and sandy white barring of these surface hairs. Dense, rather greasy fur of a very different consistency covers the pads of the very short feet. The claws and digits are short and broad.

Red rock hares are nocturnal and shy; consequently they are easily overlooked. They are recorded from several localities in the eastern Rift Valley in Kenya, from Zambia, eastern Rhodesia, South Africa and South-west Africa. They probably range through the intervening territory wherever there is suitable countryside.

They are only found in stony country where dense bush, grass and rocks are intermingled. They shelter in "forms" like other hares but these are usually situated under slabs of stone or in crevices. Shortridge (1934) collected these animals in South-west Africa and has found that he took to be their breeding places in rock crevices, which were sometimes guarded by bundles of grass and small sticks.

Their food is grasses, herbs and the shoots of shrubs. Smithers (1966) says that they first venture out after 10 p.m., to graze on open grassland close to the rocky Matopos Hills in Rhodesia. Roberts (1951) described them emerging in the late afternoon in areas of South Africa where they had not been hunted.

They are extremely wary and alert and generally hide long before they are seen. In their broken habitat they usually crouch quite still until the last moment. The only wild rock hare I have seen broke away from within a metre of my feet and had disappeared in a moment dodging through the rocks and scrub. Their gait is not unlike that of a rabbit, but they are capable of rapid and startling manoeuvres when pursued by dogs; their peculiar woolly feet must assist them to race over smooth rocks. Shortridge remarks that their normal posture is crouched, with the ears cocked forward and that the silhouette of the ears sometimes betrays them to the hunter; a hit is always accompanied by a cloud of their easily loosened fur, he says. Roberts (1951) also shot them in Natal, when they climbed onto eminences which they used as observation posts. They are entirely cryptic in colouring and no white scut or any other marking shows when they flee. Roberts, however, has described them uttering "a loud startling series of screams when racing away at night, evidently with the idea of scaring one away! These screams cannot be described as anything less than fiendish".

They deposit their dung in the same place, which is generally a flat spot among rocks. Here, Grant says, they can be readily trapped.

Bowker (1927) thought that they were usually associated in pairs. Most

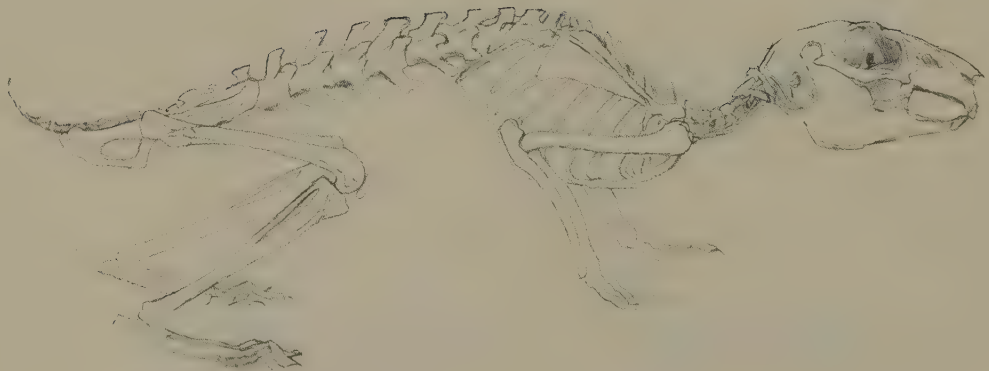


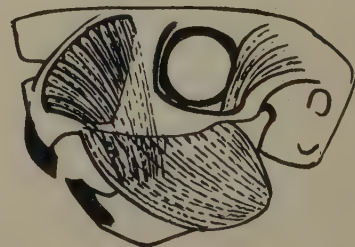
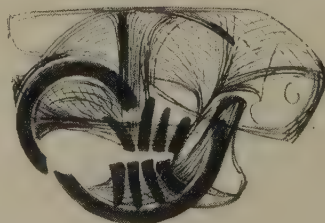
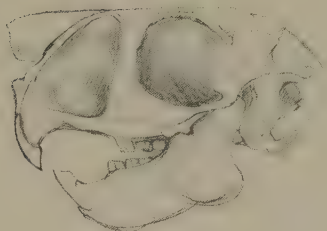
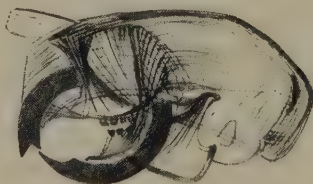
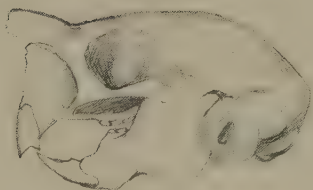
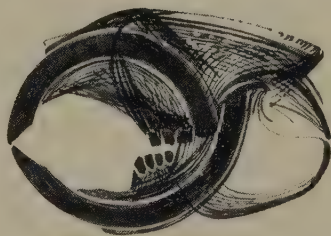
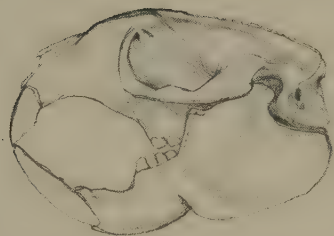
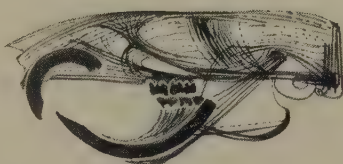
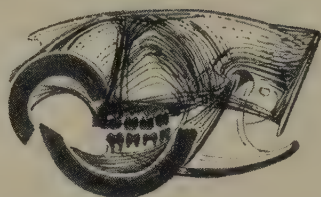
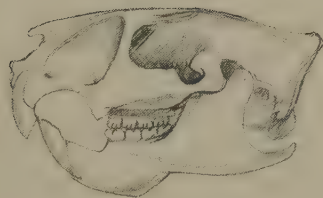
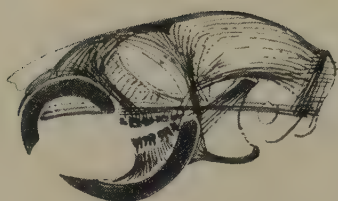
authors have described them as solitary. Shortridge found them concentrating to some extent in particularly suitable localities but without being truly gregarious. They associate very closely with hyrax and, like them, will sometimes sunbathe in the morning. They probably benefit from the hyrax' alertness as well as taking refuge in the same holes. Their habitat shelters numerous small carnivores but Shortridge observed that the dens of genets in South-west Africa were often strewn with remains of brown hares, *Lepus*, but never with those of *Pronolagus*. Perhaps their screams, their agility or, in the last resort, their impudence provide their defence. Roberts describes peering into a crevice:

"I found myself looking into the face of a red hare, lying on a ledge not a foot away; turning my head round to secure a stone to throw at it, the hare used my chest as a springboard to get away and was out of the cave in a flash. On another occasion my dog pointed to a grass-covered spit running out into a dry donga and when I walked along the spit to put up whatever might be there, one of these hares sprang right into the face of the dog, which only succeeded in smothering itself in fur while the hare raced away to a nearby koppie and safety."

The flesh of these hares is described as very aromatic. Perhaps this is due to their diet; for klipspringers probably feed on many of the same plants and they too have choicely flavoured meat.

Little is known of their breeding behaviour. Shortridge published a photograph of the young in their downy nest made from the mother's fur, and he suggests that the young carry very little scent. Bowker found one nest at the base of a hollow tree.





Rodents

RODENTIA

Sciuridae
Anomaluridae
Pedetidae
Bathyergidae
Rhizomyidae
Cricetidae
Muridae
Gliridae
Thryonomyidae
Hystriidae

Of all the mammalian orders the rodents contain the largest number of species. In East Africa they account for nearly 28 per cent of the mammal species.

The most obvious common feature of rodents is their prominent gnawing teeth, two incisors in each jaw with a long space or diastema before the cheek teeth. The body build of most rodents is that of relatively conventional quadrupedal animals but burrowing, bounding, gliding and climbing have modified the shape of various groups.

The chisel-edged gnawing teeth of rodents dominate the structure of their skulls for the teeth must grow continuously to make up for wear, and be well anchored to stand up to stress and strain. Their action is consequently separate from that of the molars so that when a rodent gnaws, the molar teeth no longer occlude and the articulation of the lower jaw must accommodate to this functional dislocation.

The incisors form arcs that are built right back into the head and jaws. Their semi-circular form imparts structural strength and is also a product of geometrically regular growth. The various forms of anchorage provided for rodents' incisors are very interesting and the position of these teeth in relation to the molars is very variable. The drawings of cut-away skulls (opposite) illustrate how these chisel-teeth are set in the matrix of the skull in different forms. Although dramatic differences of form are apparent the arrangements shown are mainly related to mechanical function which can vary within the larger groupings of rodents.

Where there is a major phylogenetic implication, however, is in the masticatory musculature. In all rodents the masseter muscle is very highly developed and divided into two parts: the more superficial or lateral sheet of muscle is for fore and aft movement while the deeper (medial) sheet controls vertical movement. The differentiated functions of the masseter allow it to serve the incisors for gnawing and also the molars for grinding. The three main rodent divisions, the sciuromorphs, the hystricomorphs and the myomorphs, show distinctly different structural arrangements of the masseter.

The most conventional organization is that found in the sciuromorphs, where part of the masseter is attached to the back of the zygomatic arch and part to the front. However, the need for strong fore and aft leverage has extended the anterior part of the masseter to near the bridge of the nose and the maxillary process forms a long oblique channel to accommodate this muscle.

Squirrels are arboreal forms and are dependent upon well-developed

◀ Sciuromorph
(*Funisciurus lucifer*).

◀ Hystricomorph
(*Thryonomys gregorianus*).

◀ Myomorph
(*Cricetomys gambianus*).

◀ Bathyergid
(*Cryptomys mechowii*).

◀ Anomalurid
(*Idiurus zenkeri*).

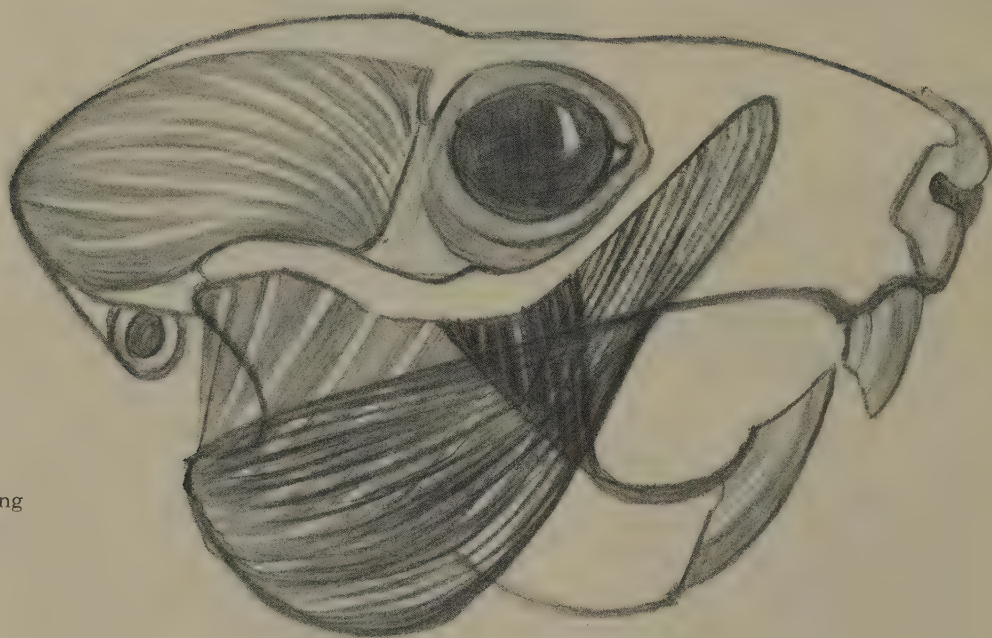
◀ Pedetid
(*Pedetes caffer*).

1st Column. Skull profiles of some important rodent groups.

2nd Column. Diagram showing tooth roots and direction of bony buttressing.

3rd Column. Diagrams of masticatory muscles.

Head of *Protoxerus stangeri* indicating the attachment and direction of the masticatory musculature.



vision and it is perhaps for this reason that the orbit has not been invaded or disturbed by muscle. This is not true of most other rodents, which have to stop chewing if they are to see properly, because the presence of large muscles underneath the eyes tends to jog them about. Hystricomorphs depend on smell most and, in this group, the anterior part of the masseter runs close to the eye but at a relatively low angle. The maxillary process has divided so that the zygomatic bridge acquires three distinct bases, a slender one near the front edge of the toothrow, a stouter one above and in front of the eye and the usual attachment behind to the squamosal.

The Myomorph orbit is also invaded by muscle, but here the medial masseter has pushed up at a high angle through the infra-orbital canal and on to the barrel of the nose, so that the upper branch of the maxillary process is generally more slender than the lower branch, which forms the flat zygomatic plate.

The recognition of these three types has conveniently simplified taxonomy on the one hand, but, on the other, it has created special problems for the classification of those rodents that don't fit neatly into any of these categories. Of East African rodents, the Anomaluridae, the Pedetidae and the Bathyergidae are in the position of *incertae sedis*. Palaeontology has revealed no common origin for the rodents, no fossils that might link even the families, so that, for the time being, they must be treated piecemeal as a series of discontinuous groups, connected mainly by their common specialization of gnawing incisors.

The molars are very varied in structure. Some, like those in the Bathyergidae, are simplified pegs; others are immensely complex, through the development of numerous high ridges which form loops and laminations when they become worn. These structures are thought to have derived originally from the primitive mammalian four-cusped tooth.

Because teeth are central to our understanding of rodent relationships, I have illustrated the upper molars of most genera but have generally avoided description as this involves a sophisticated vocabulary which is intelligible to few non-specialists. However, within the major rodent groups it is quite easy to appreciate degrees of morphological resemblance between the teeth of one form and another and the illustrations may be helpful. It should be pointed out, however, that the worn teeth of old animals seldom give any clue to structure, particularly in the rodents of this area, where all species have rooted teeth which wear out completely with old age.

The rodent's primary dental specialization is that of a gnawing herbivore but in the course of evolution rodents have diversified their diets to include animal foods, roots, fruit and seeds and several broad trends are apparent as well as countless refinements. Insectivorous rodents tend to have sharp-cusped molars and long muzzles. True herbivores, instead, tend to have broad incisors and mill-like grinding teeth with appropriately stout skulls to support them. The omnivorous types tend to fall in between the two. (The common rat is a good example of this generalized type.)

For the field-worker in East Africa, rodents will be met with as members of communities rather than as isolated species, and a row of traps set in any habitat will generally harvest a variety of species belonging to various morphological types. The table overleaf lists some of the genera and species that may be encountered in various habitats. Both the environment and the rodents' adaptive role are of course very much more complex than can be expressed in a generalized table nonetheless the recognition of diverse rodent niches is crucial to their study.

Rodent densities can reach extraordinarily high proportions and several workers have tried to estimate the biomass of small rodents in various habitats and under various conditions. Estimates range from a maximum of 60 kg per hectare (Verschuren, 1966), 13 to 16 kg per hectare (Dieterlen, 1967a), 3 to 8 kg per hectare (Misonne, 1963) to 1.7 kg per hectare (Bellier, 1967). It is quite clear that in spite of a wide range of variation in densities the ecological role of rodents is far from negligible, particularly in the thicker and moister types of vegetation.

Few species have received adequate attention in relation to their feeding habits and the information given in the profiles is mostly gathered from scattered records.

Many species circulate their food twice through the gut. The species that have this habit die when prevented from eating their pellets (caecotrophs) and it is thought that the breakdown of cellulose by bacterial action in the caecum probably produces metabolites which can only be absorbed by being recycled.

It is often assumed that food surplus encourages the dreaded population explosions that some smaller rodent species are prone to. That this may not be so was suggested by some experiments by Crebbs and De Long (1965) on

RODENT NICHES

<i>Habitat</i>	<i>Herbivores (and frugivores)</i>	<i>Unspecialized omnivores</i>
Forest	<i>Beamys</i> <i>Cricetomys</i> <i>Hybomys</i> <i>Atherurus</i>	<i>Praomys (Praomys)</i>
Secondary growth	<i>Cricetomys</i> <i>Otomys</i> <i>Atherurus</i>	<i>Praomys (Praomys)</i> <i>Mus triton</i>
Moist savannas and woodlands	<i>Otomys</i> <i>Mylomys</i> <i>Lemniscomys</i> <i>Hystrix</i> <i>Thryonomys gregorianus</i>	<i>Aethomys</i> <i>Mus triton</i> <i>Praomys (Mastomys)</i>
Marshes	<i>Dasymys</i> <i>Rhabdomys</i> <i>Otomys</i> <i>Pelomys</i> <i>Delanymys</i> <i>Thryonomys swinderianus</i>	<i>Mus bufo</i> (high alt.)
Dry savannas and woodlands	<i>Saccostomus</i> <i>Arvicanthis</i> <i>Lemniscomys</i> <i>Hystrix</i> <i>Thryonomys gregorianus</i> <i>Tatera</i>	<i>Praomys (Myomyscus)</i> <i>Praomys (Mastomys)</i> <i>Mus minutoides</i> <i>Aethomys</i> <i>Steatomys</i> <i>Xerus</i>
Grassland	<i>Arvicanthis</i> <i>Tatera</i> <i>Rhabdomys</i> (high alt.) <i>Otomys</i> (high alt.) <i>Pedetes</i> <i>Gerbillus</i>	<i>Xerus</i> <i>Steatomys</i>

(excluding subterranean forms)

Specialized omnivores and insectivorous forms

Deomys
Malacomys
Colomys
Lophuromys sikapusi
Lophuromys flavopunctatus
Funisciurus (*Funisciurus*)
Lophiomys (in dry forest)

Climbers

Squirrels
Praomys (*Hylomyscus*)
Thamnomys
Graphiurus
Anomalurids

Lophuromys woosnami (high alt.)
Lophuromys flavopunctatus

Squirrels
Praomys (*Hylomyscus*)
Oenomys
Dendromus mystacalis
Grammomys
Thamnomys
Graphiurus

Lophuromys sikapusi
Uranomys
Zelotomys

Squirrels
Dendromus mesomelas
Grammomys
Graphiurus

Colomys
Malacomys
Lophuromys flavopunctatus

Dendromus mystacalis

Zelotomys
Acomys

Squirrels
Grammomys
Thallomys
Dendromus melanotis
Graphiurus

Lophuromys flavopunctatus (high alt.)

Dendromus mesomelas (high alt.)

a species of vole that usually fluctuates in numbers. The provision of more food than the voles could eat lead to no exceptional growth of numbers, so that food quantity alone does not answer the question of what controls population cycles. Taylor (1972) investigating an outbreak of rats in Kenya farmlands during 1962 thought that a greatly extended rainy season in the previous year encouraged a longer period of plant growth and that this prolonged the rodents' breeding seasons. The densest populations (of *Arvicanthis*, *Praomys natalensis*, *Rhabdomys* and *Dasymys*) were found in unweeded fields and areas of thick herbage. That greenstuff might provide a trigger to breeding has been shown by Weinbrenn and Mason (1957), who induced fecundity in a non-breeding colony of *Arvicanthis* by adding greenstuffs to their diet. Work on this problem would have wide implications for our understanding of rodents and their control. Indigenous rodents have already acquired destructive habits in some areas of intensive cultivation and silviculture and with the expansion of agriculture their study and control will become more important.

In addition to their role as pests some species of rodents are a threat to health, the principal culprit being the introduced rat. The appearance of African rodents in laboratories is increasingly common and Davis (1963) has reviewed the contribution of several species to medical research.

In common with most mammals a large part of the rodent's life revolves around scents, particularly glandular secretions. The importance of this aspect of their biology is obvious to an observer of rodent behaviour. For instance, squirrels and rats frequently exhibit greater interest in strange scent deposits in their surroundings than in a strange animal close to them: social disruption often follows cleaning out of the cages of captive rodent groups, betraying that the scent marks are crucial tokens in the animals' sensation of their own and their fellows' identities. In large mammals the role of scents becomes more accessible to human perceptions (Vol. III) but most rodents are no less dependent upon the information (and probably the sense of security) provided by glandular and other body scents.

Squirrels

Sciuridae

The name squirrel is an anglicization of the Greek word "skiouros", which means "shade tail". The often spectacular tail of squirrels is their most immediately striking feature and one that plays a uniquely important role in the life of these animals. Otherwise the squirrel does not appear to be a very remarkable rodent; it has an active demeanour, a round, blunt head, with relatively large eyes and rather generalized limbs and feet. Sometimes the body carries bold longitudinal stripes or it may be dramatically coloured with red tints on the limbs, head and tail. The hair may be soft, as in some of the *Funisciurina* or coarse as in the ground squirrel.

The acquisition of agility in the trees and a special capacity to cope with difficult foods associated with trees, mainly nuts and other vegetable matter, seem to have earned them an almost world-wide distribution.

In spite of what would appear to be rather specialized habits, they have structural peculiarities in the skull which show that, of living rodents, they are closest to the more generalized ancestral stock of all rodents. The retention of two upper premolars and a lower one is a primitive trait, as is also the relatively simple arrangement of the masseteric muscle groups.

Although their weights range between about 20 and 3,000 g in arboreal forms, and up to seven kilograms in the ground dwelling marmot, squirrels do not depart far from a common body plan. This is particularly true of the tree squirrels, of which Moore (1959) says:

"... conservatism in tree squirrels suggests that the tree squirrel niche must be extremely exacting in anatomical requirements. It implies further that the selection in this severely conservative role must also be extremely similar in various parts of the world. The similarity between ordinary tree squirrels of tribally separate stocks, and the scarcity of important skull character differences between them ... implies that tree squirrels were well adapted to their niche very early".

The fossil record shows that they were established in Eurasia and North America by the Miocene, at which time they probably also invaded Africa. South America was invaded much later, in the Pleistocene. A Eurasian origin for squirrels is also betrayed by the presence there of some 33 relatively diverse genera, mostly living in South-east Asia. Africa instead has eight genera belonging to three tribes, the Xerini, the *Funambulini* and the *Protoxerini* (see table below, after Moore, 1959):

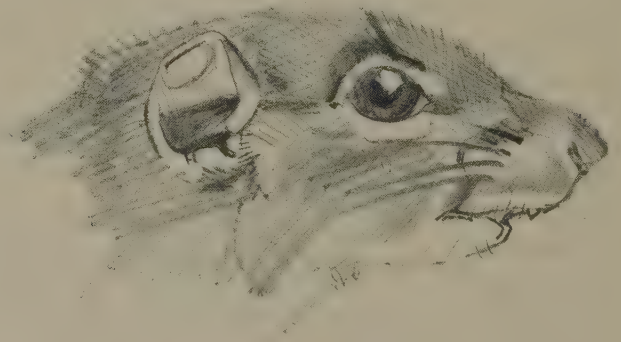
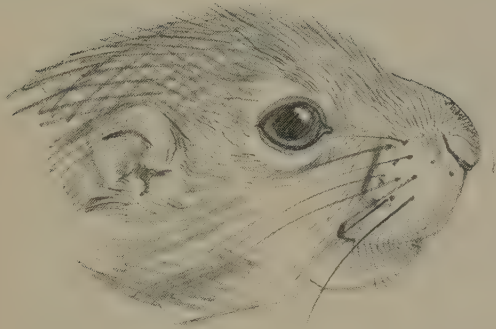
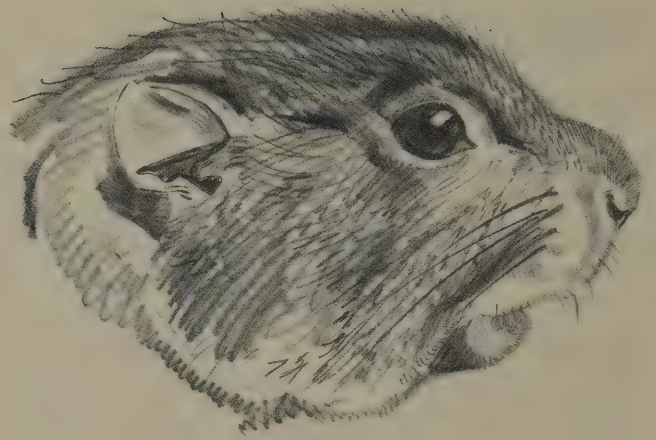
Xerini: *Xerus*, *Atlantoxerus*, *Spermophilopsis*.

Funambulini: *Funambulus*, *Funisciurus*, *Myosciurus*.

Protoxerini: *Protoxerus*, *Epixerus*, *Heliosciurus*.

With the exception of the Indian *Funambulus* and the Persian *Spermophilopsis*, the genera contained within these three groups are exclusively African and it is probable that they share a common origin.

The African tree squirrels have long orbits, a narrow interorbital breadth and short infraorbital canals. Moore (1959) concludes that the *Funisciurina* are the nearest relatives of the *Protoxerini*. He goes on to say:



"One needs at least to consider the possibility . . . that Ethiopian tree squirrels evolved from the ground squirrel stock which now survives in Xerini. The long orbits and the short interorbital breadths of the Protoxerini and Funisciurina suggest this. The separation of the buccinator foramen from the masticatory foramen in *Heliosciurus* and *Epixerus* of the Protoxerini, and *Xerus* and *Ailantoxerus* of the Xerini lends this suggestion further support. Also the masseteric tubercles of *Heliosciurus* are remarkably like those of the Xerini".

◀ *Protoxerus stangeri*.

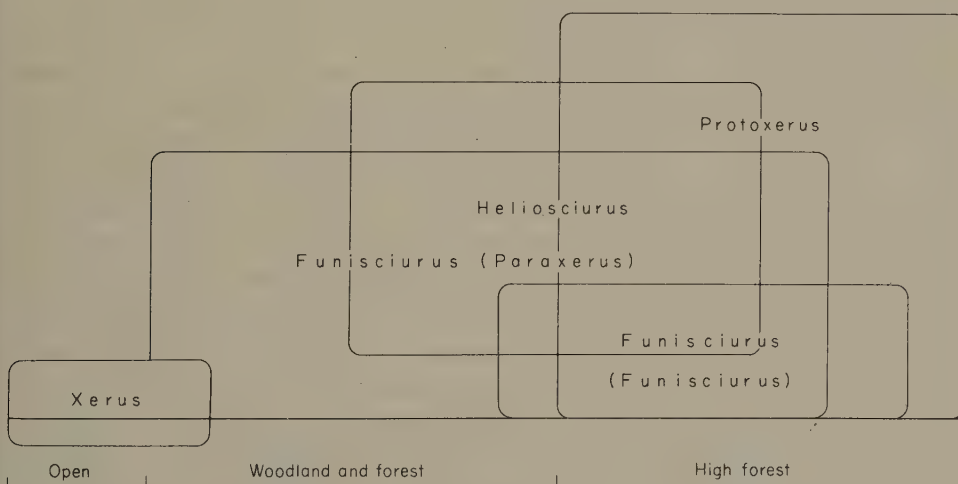
What is known of the fossil record tends to strengthen Moore's suggestion. Forest connections between Africa and Eurasia undoubtedly existed in the late Oligocene and early Miocene, but all later connections seem to involve exchanges of fauna adapted to relatively dry conditions. Squirrels are not known until the late Miocene. Before that time their niche was probably occupied by the Anomaluridae, and the very rare relic species *Zenkerella* may give us some idea of an original African "squirrel" type.

◀ *Heliosciurus ruwenzorii*.

The Eurasian squirrels have differentiated into numerous distinct forms: various intermediates between the giant squirrel and the tiny pigmy squirrels, brilliantly coloured and patterned squirrels, striped squirrels and plain squirrels, solitary and gregarious squirrels, rock squirrels, palm squirrels, ground squirrels and long-nosed insectivorous squirrels. They provide an interesting contrast with the African squirrels, because the latter too have diverged from one another, but having started more recently, probably from a common stock, they have more in common with one another, and their specialized traits are less exaggerated. The situation has some resemblance with the "late start" of Darwin's finches in the Galapagos.

There is a large high-forest canopy squirrel, *Protoxerus*, exhibiting some of the traits of the Oriental *Ratufa*. There is a pigmy squirrel in West Africa, and the various intermediate species probably specialize to some extent, according to the types of fruit or nuts they eat. *Funisciurus* (*Funisciurus*) appear to be incipient insectivorous types and some elongation of the muzzle is apparent.

◀ *Funisciurus* (*Paraxerus*) *lucifer*.



◀ *Funisciurus* (*Funisciurus*) *pyrrhopus*.

◀ *Xerus rutilus*.

Diagram showing ranges of elevations and habitat types commonly used by squirrel genera.

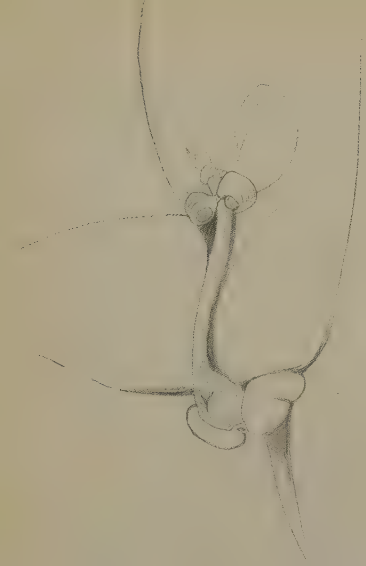


Figure 1. Surface dissection of *H. rufobrachium* showing penis and anal glands. The heads of the epididymis show through the "collars" on either side of the penis and the position of the testes (inside the abdominal wall) is indicated.



Figure 2. Diagram of a deeper dissection showing the anal gland "unwound" and one testis with its accessory structures (within the abdominal cavity).

Many African species are known to store food in their nests. Carrying food to a hiding place is clearly an innate behaviour pattern for most, if not all, squirrels, although the advantages of storing food in the tropics are less obvious than in temperate zones. Young squirrels push bits of food into crevices at an early age. The Eurasian *Sciurus vulgaris* has been observed to mark large food caches.

The use of glandular secretions, common perhaps to all squirrels, is a largely unknown aspect of their biology. I have found pairs of large anal sacs in sexually active males of *Heliosciurus rufobrachium* and also *Funisciurus (F.) pyrrhopus*. A captive of the latter species has been observed to follow a cycle in which both the glands and the testes undergo a periodic increase and decline in size. The activity of the anal glands and the frequency of anal marking seemed to be correlated with the size of the testes, and there can be little doubt that the glands have an important role in sexual behaviour. The secretion is produced by a complex of sebaceous, holocrine and apocrine glands enclosed by a muscular envelope and has very little scent to the human nose. Like soft candle grease in appearance, it can be squeezed out of the ducts as if from a tube.

Scent is probably of special importance in their sexual life, as well as in the detection of food; but Cansdale has noticed differences in the ability of *Heliosciurus* and *Funisciurus* to smell insects hidden in detritus, the latter tracing the insects without hesitation, the former apparently unaware of their presence (Rosevear, 1969).

Sight is undoubtedly their most important sense. For the effective exploitation of their demanding arboreal environment, for the evasion of enemies and for seeking food, accurate, alert and discriminating vision is essential. For their social life too, it is crucial and the development of conspicuous tails is probably linked with the primacy of vision.

The original balancing role of the tail seems to have become augmented by its role as signal. Tails are of the greatest importance in squirrel communication and the "language" of tail waving has broad similarities in many species, although for the sun squirrels, some of which have thin, rather plain tails, they may be less important.

Courtship behaviour will be discussed below, but one component of male sexual behaviour can be mentioned here; it is a rather slow, circular movement of the tail. In *Funisciurus (Funisciurus) pyrrhopus* this takes the form of a geometric curl above the displayed genitalia (see drawing, above, opposite). In encounters between squirrels and in sexual and other chases, the tail is often jerked in a stiff manner or vibrated. Alarm before flight is signalled by quick fore and aft waving, while in the face of slightly unfamiliar situations where there is some tension, the tail is raised over the back. These altering postures and movements can radically alter the visual impact of the signal. To illustrate this the tail of *Protoxerus* can be examined. When a male of this species is sexually excited and chasing the female, the hair of the tail stands on end, creating an incandescent effect, with a white halo round the black and white flecked tail. However, when the tail is raised against the back and the hairs fan out from the vertebrae, a series of fine vertical stripes appear in black and white, running the length of the tail. This pattern is the exact reverse of the pattern displayed when the animal is climbing with its tail relaxed



a. *P. stangeri*, upper side of tail.
b. *P. stangeri*, under side of tail.
c. *F. pyrrhopus*, tail curl.

and lying behind in line with the body. The tail is then black with widely spaced white bars across the tail and a white edge trims the margins.

Squirrels have good hearing, in spite of all the African genera having relatively small pinnae. This characteristic may also lend some support to the idea that African squirrels derive from a ground squirrel stock.

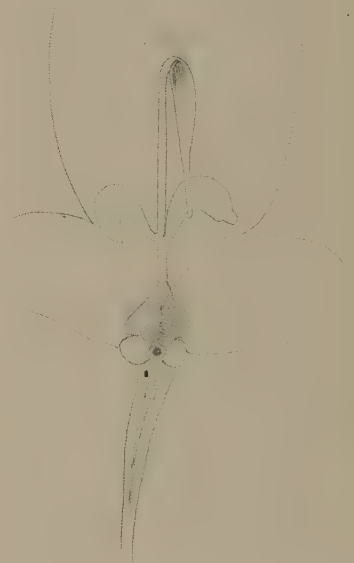
They have a wide repertoire of noises, scolding chatters, sexually excited purring, squeaks and pipings as well as screams and growls of pain or anger. Most squirrels occasionally make strange long-distance calls, which will be discussed below.

The predators of squirrels are numerous; they are principally the small carnivores, such as genets and the arboreal mongoose, *Herpestes* (*Myonax*), snakes and raptorial birds. The hawk-eagles, *Heiraaëtus dubius*, *Hieraaëtus africanus* and the long-tailed hawk *Urotriorchis* appear to favour squirrels as prey. Escape behaviour may involve spiralling around branches or, when pursued, headlong flight.

African squirrels appear to have a variety of quite different social structures; some seem to be relatively gregarious, others solitary. The following profiles will show how much remains to be learnt.

Sexual behaviour is one of the least understood aspects of squirrel biology. This is partly due to the startling rapidity with which squirrels go through complicated action patterns and to the difficulties of observing them.

Only a generalized sketch of their reproductive behaviour is possible, made up from scattered observations of various squirrel genera. It will already be apparent that the courtship of squirrels involves many components. Certain tail postures have already been shown to play a definite role. The link between glandular secretions and sexual condition in some species has been described and loud contact cries have been mentioned.



Genitalia and anal glands of *F. pyrrhopus* showing structure of penis.



It is possible to discern some ecological zonation in the squirrels represented in East Africa which broadly coincides with the genera. *Xerus* is a ground-dwelling genus that occurs in relatively open habitats. *F.* (*Funisciurus*) lives on the ground, mostly in forest among low vegetation. *F.* (*Paraxerus*) inhabits the widest range of vegetation levels and types. *Heliosciurus* is more arboreal and *Protoxerus* is a canopy squirrel (although it also feeds readily on fallen fruits off the forest floor). If African squirrels had terrestrial or semi-terrestrial origins one might expect to find traces of an orthogenetic return up into the trees. In which case, could the pattern sketched out on p. 371 have any correspondence to an evolutionary hierarchy?

Dr John Backman wrote to Audubon in 1839: "the ever-varying squirrels seem sent by Satan himself to puzzle the Naturalists". This variation makes the study of squirrels very difficult but also very interesting. Their colouring is very responsive to climate, and clines can be observed in the coat colour of some species. Racial divisions are less meaningful in those species with a continuous clinal distribution than in the populations of species with discontinuous distribution. The most complex problems are raised by those groups that have been subjected to the effects of climatic change or that have been isolated by rivers or other natural barriers. In these cases distinct populations may lead by perceptible steps, from race to race, until a separate species is betrayed by its sympatry with some other closely related form. Situations of this sort can be found amongst the *Funisciurus* (*Funisciurus*) group. They await a more exact definition of the nature of this speciation process.

I have come across another difficulty in assessing the validity and meaning of the named races and species. Hybridization between two distinct species appears to be the only explanation for an extraordinary multiplicity of races in the southeastern corner of Africa. It is possible that other cases of hybridization may occur in the main forest block and elsewhere.

The zoogeography of African squirrels suggests that many species are mutually exclusive over big areas, but can coexist in some localities where there is presumably a differentiation of niches. These situations need study and definition.

The general biology of squirrels has many common features. Most, if not all, squirrels build nests of some sort, but those in habitats that lack concealment or suffer from seasonal fires or drought, tend to use holes in trees or in the ground. The local abundance of such species may depend as much on the availability of such shelters as upon food supplies. Nests are built over several days and are generally started by the weaving of a well-attached platform, followed by the building of the sides and roof out of various twigs and fibres. The inside is often lined with finely prepared material, which may be brought by mouth from some distance away, in carefully teased and portable bundles. Dummy nests are made by some Palaearctic species.

Foods range from hard nuts to soft fruits, pods and most other forms of vegetable matter, e.g. bark, stems, resin, roots, buds, leaves and flowers. Animal matter, mainly insects, is eaten by most species, but the *Funisciurina* eat insects more than the other genera.

Most species pluck and gnaw their food, manipulating it ably in their

◀ Skeleton and dissection of *Xerus erythropus*.

hands. The structure of the hand is subject to considerable differences between genera and the differences are probably correlated with various manipulative patterns and also the locomotory idiosyncrasies of species. All arboreal species have sharply curved claws for climbing, and the ground squirrels stout pointed ones for digging.

Certainly very emphatic postures, scents and sounds must all be employed to achieve effective reproduction in animals that are, on the evidence available, widely dispersed and often highly territorial. In *Sciurus vulgaris* territories are held by both males and females and are separately maintained for a large part of the year. In Spring, the males invade female territories, and the invader chases and threatens the female until his presence is accepted in her territory. The timing of sexual behaviour in African squirrels depends upon the onset of male cycles and female oestrus. Nothing is known about what determines these cycles. In some species territories are permanently shared by both sexes, but chasing seems to be common to all squirrels. However, the females of some African species, like juveniles playing, give every appearance of inviting the chase by "presenting".

Most species of squirrel make a loud call. Eibl-Eibesfeldt (1958) has suggested that the male *Sciurus vulgaris* draws out the female's readiness for contact because the call resembles that of the young. The call might derive from a juvenile "want" call, but there is no sexual distinction as to the caller and the response where many African species are concerned. The noise may not always play quite the same role, but the evidence suggests that it is usually a mutual contact call made in the mating season, which advertises the caller's condition and serves to bring widely dispersed animals together. The squirrels are often less alert while they are engrossed in making this call, sitting in a frozen posture, but sometimes making treading movements with the forepaws or small flicks of the tail. The mountain squirrels make loud ringing calls and in many species individuals cluck at each other. The strange "gong" call of *Protoxerus* may also be derived from this contact call.

Once close contact between the sexes has been achieved, the male deliberately postures and slowly flags his tail in front of the female. The female's retreats become more and more symbolic, until the flight movement becomes a turning away with tail lifted, and a urine trail draws attention to her readiness for contact. Copulation is achieved after several hours or, sometimes, several days of courtship. In *F. (P) ochraceus*, where territories are apparently shared between several animals of both sexes, the female mock-mounts the male.

Basic similarities can be perceived in the sexual behaviour of most East African squirrels, but the strength of their various responses to visual, olfactory and auditory stimuli could perhaps be correlated with the development of glands or coat patterns, and with such easily observed differences such as relative noisiness, tameness or conspicuousness. Here lies a rewarding field of enquiry.

Squirrels are seldom numerous enough to constitute a serious menace, but with silviculture and agriculture becoming increasingly specialized and intensive, it is probable that some species will become a nuisance in some areas.

A possible health hazard posed by the ground squirrel is discussed in the profile of *Xerus erythropus*.

Funisciurine Squirrels

Funisciurinae



F. (P.) lucifer.

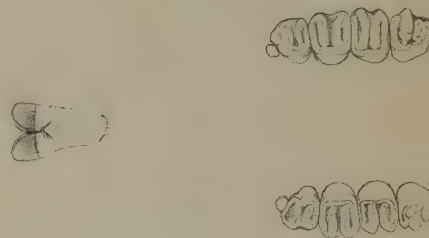
Two groups of African squirrels, *Funisciurus* and *Paraxerus* were united by Moore (1959) in a subtribe Funisciurina. *Funisciurus* was first named by Trouessart (1880), *Paraxerus* by Major Forsyth (1893) but a close relationship between the two has been recognized from an early date. Thomas (1909) said *Funisciurus* "would seem to be the representative of *Paraxerus* in the West African forest region". This can now be seen to be a slightly oversimplified statement of the situation but is broadly true.

A peculiar enamel pattern has been the principal character held to separate the genera. How tenuous a characteristic this is can be appreciated by reading a recent key to the African squirrels (Amtmann, 1966b). The distinction is made here that in *Funisciurus* the cheek teeth "of both upper and lower jaws are more or less flat-crowned in adults". This contrasts with the cheek teeth of the lower jaw in *Paraxerus* "being cuspidate in adults (although upper ones may be more or less flat-crowned)". Having attempted to study East African squirrels on the basis of a clear cut division between these genera I have found their generic separation untenable.

The problem revolves around one species, *Funisciurus carruthersi*, which has emphatically flat-crowned teeth. On the basis of other evidence (which will be presented below) it seems clear that this squirrel's closest affinities are with a species of *Paraxerus*, the lower teeth of which are "more or less" cuspidate. While I am unable to explain the slightly different pattern of tooth-wear between the two species, the evidence for their phyletic relationship on



Upper tooththrows *F. (P.) l. byatti*.



Upper tooththrows *F. (P.) carruthersi*.

other counts is so overwhelming that a common genus seems imperative. However a revision of the generic status of *carruthersi* must bring into question the usefulness, indeed the validity, of separating these genera on the basis of "more or less" flat-crowned lower cheek teeth.

There is one other diagnostic feature in the traditional keys: two pairs of mammae in *Funisciurus* and three in *Paraxerus*. The one female *carruthersi* I have had the opportunity to examine had three pairs of mammae, but it should be remembered that this is an unstable factor in some rodents. For instance, a specimen of *byatti* in the National Museum, Nairobi, has four mammae on one side and three on the other.

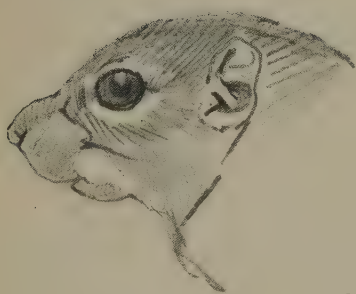
The most immediate evidence for *carruthersi*'s relationship with a Tanganyika mountain squirrel, *byatti*, is their very close resemblance (see colour plate, p. 383). This superficial resemblance is more than skin deep, for a comparison of their skulls shows that their proportions and detailed conformation are almost identical and radiographs of their skulls have failed to reveal any important divergence of form. Moore (1959) used the number of transbullar septa as an important criterion for squirrel classification. According to his table all *Funisciurus* have one pair of septa, while *Paraxerus* have one, one and a half or two; *carruthersi* has one pair of poorly developed septa and more than a trace of a second one. This arrangement agrees closely with that of *byatti*, whereas *Funisciurus pyrrhopus* has one pair of fully developed septa with only the slightest trace of a second. According to Moore's criterion both *carruthersi* and *byatti* would rate one and a half septa. Turning from comparisons of *carruthersi* with *byatti* to comparisons with undisputed *Funisciurus* species it is immediately obvious that this form occupies a lonely position.

Rosevear (1964) described and defined four major groups within *Funisciurus* which could all be ordered into a cline with a "complete intergradation from the small *isabella* Gray at one end to the large *pyrrhopus* F. Cuvier at the other"; *carruthersi* fell outside this scheme and was effectively ignored in this review.

a. *F. (F.) pyrrhopus*.

b. *F. (P.) carruthersi*.

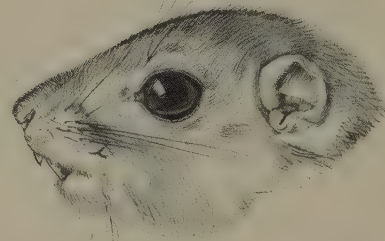
c. *F. (P.) lucifer*.



a.



b.



c.

The ecological evidence is most compelling: *carruthersi* inhabits the montane forests that stretch intermittently from Lake Tanganyika to the Ruwenzori mountains. Faunal affinities between these mountains of the Central Refuge and those of Tanzania, where *byatti* occurs, can be demonstrated for very many species of animals and plants (see Vol. I, pp. 69—75). It can also be shown that the links between these areas have been broken for a very long

period of time and that there are various degrees of differentiation between the related forms of these regions.

At this point another species of squirrel enters the discussion. Almost all the montane habitats of tropical Africa, although separated by vast areas of lowland, have had connections of some sort in the distant past and the Cameroon Mountains have numerous faunal and floral elements in common with the East African mountains. In 1950 Hayman described a new mountain forest squirrel, *cooperi*, from these very isolated montane forest remnants of the Cameroon Highlands. This species has a shorter nose and a narrower palate than *carruthersi* or *byatti*. It is also smaller, but it is otherwise very similar to its ecological equivalents (and probable relatives) to the east. It has an even greater resemblance, however, with a still smaller West African lowland forest species, *poensis*, which has been allocated successively to *Sciurus* (Smith, 1834), *Funisciurus* (Thomas, 1906b), *Paraxerus* (Amtmann, 1966b) and *Aethosciurus* (Rosevear, 1969).

It may be appropriate at this point to illustrate the taxonomic uncertainty that has surrounded the status of these animals for many years. The table below is telling evidence against the traditional generic system, exposing how subjective diagnoses can be when the criteria are inadequate.

<i>carruthersi</i> (Thomas)	<i>Funisciurus carruthersi</i> (Thomas, 1906b)
<i>cooperi</i> (Hayman)	<i>Heliosciurus (Aethosciurus) cooperi</i> (Hayman, 1950)
	<i>Paraxerus cooperi</i> (Amtmann, 1966b)
	<i>Aethosciurus cooperi</i> (Rosevear, 1969)
<i>byatti</i> (Kershaw)	<i>Funisciurus byatti</i> (Kershaw, 1923)
	<i>Paraxerus byatti byatti</i> (Swynnerton and Hayman, 1951)
	<i>Paraxerus vexillarius byatti</i> (Amtmann, 1966b)
<i>lucifer</i> (Thomas)	<i>Xerus (Paraxerus) lucifer</i> (Thomas, 1897)
	<i>Sciurus lucifer</i> (Thomas, 1909b)
	<i>Aethosciurus lucifer</i> (Allen and Loveridge, 1933)
	<i>Heliosciurus (Aethosciurus) lucifer</i> (Swynnerton and Hayman, 1951)
	<i>Paraxerus lucifer</i> (Amtmann, 1966b)
<i>cepapi</i> (Smith)	<i>Sciurus cepapi</i> (Smith, 1836)
	<i>Funisciurus cepapi</i> (Thomas, 1897)
	<i>Paraxerus cepapi</i> (Wroughton, 1909)
<i>palliatus</i> (Peters)	<i>Sciurus palliatus</i> (Peters, 1852)
	<i>Macroxus annulatus</i> (Gray, 1873)
	<i>Funisciurus palliatus</i> (Thomas, 1906b)
	<i>Paraxerus palliatus</i> (G. M. Allen, 1939)

It looks as though this confusion and profusion of genera has obscured the natural groupings of the *Funisciurina*, for when looked at as a whole, groupings and radiations appear, so that some sort of genealogical position can be suggested for every species. This has already been attempted by Rosevear (1964) for one radiation, that of the soft-furred, striped *Funisciurus* species.

It is proposed in this work to treat *Paraxerus* as a subgenus of *Funisciurus* placing *carruthersi* together with *byatti* in this taxon, recognizing only the

striped, soft-furred squirrels as *Funisciurus* (*Funisciurus*).

This enlarged group of funisciurine squirrels ranges over most of the continent south of the Sahara. Almost all the recognizable subgroups seem to contain small striped species, which suggests that a common ancestral stock might have resembled such species in some particulars.

Of these small squirrels three are particularly close: *poensis*, *boehmi* and *ochraceus*. Between them they straddle tropical Africa and they may represent



three slightly differentiated geographic forms of common derivation; their skulls, for instance, are almost identical in structure. A peculiarly isolated southeastern species, *flavivittis*, is also rather similar. The dwarfed *alexandri*, may be a relic species and also has some resemblance with *boehmi*.

In size and colouring there is a very striking external resemblance between *F. (P) boehmi* and the two species *isabella* and *congius* of the *Funisciurus* (*Funisciurus*) radiation. *F. (F) pyrrhopus* is the only representative of this radiation recorded from East Africa.

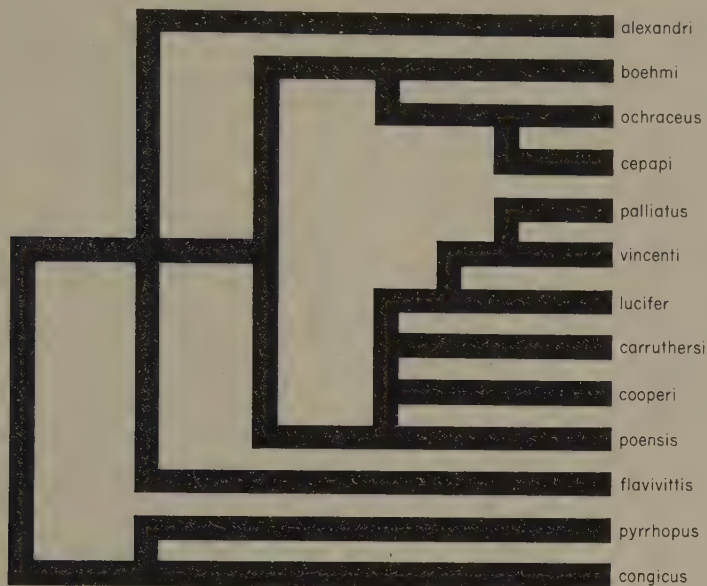
Seen in the context of eastern Africa the isolation of the endemic montane squirrels can be understood to be simply the product of climatic change. When the more westerly species, *carruthersi* and *cooperi*, are taken into account the possibility must be raised that the African montane squirrels might represent the highly fragmented relics of a formerly more widespread or even dominant group that has subsequently diverged in isolation.

The radiation of the montane squirrels appears to be very ancient. This is suggested in the first place by the differentiation that has occurred; *carruthersi*, *cooperi* and *lucifer* having evolved well-defined specific peculiarities in each case. In addition to this the *lucifer* stock appears to be ancestral to another species.

As I remarked in Volume I (p. 72), there appears to have been no recent exchange of forest species between the eastern forest relicts and the main forest block. The Tanganyika mountain squirrels are typified by *byatti* from the mountain forests of northern and eastern Tanzania. In the Livingstone Mountains east of Lake Malawi lives *laetus*, a larger, redder race with a thick strongly patterned tail. A bright red and black squirrel, *lucifer*, replaces *laetus*

in the very wet mountainous area at the northern end of Lake Malawi. Its colouring is an extension and intensification of the erythristic tendency exhibited in *laetus*; all these forms are treated as one species here.

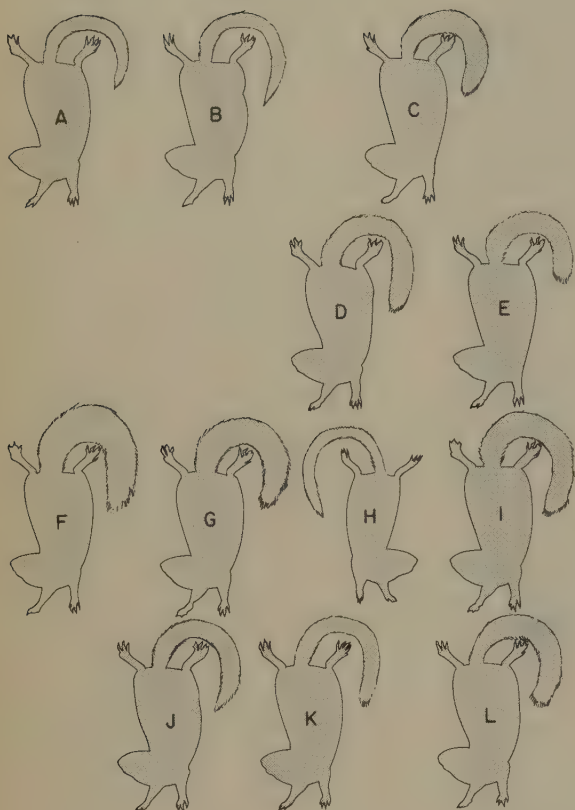
Far to the south of *laetus* are two further montane squirrels which might



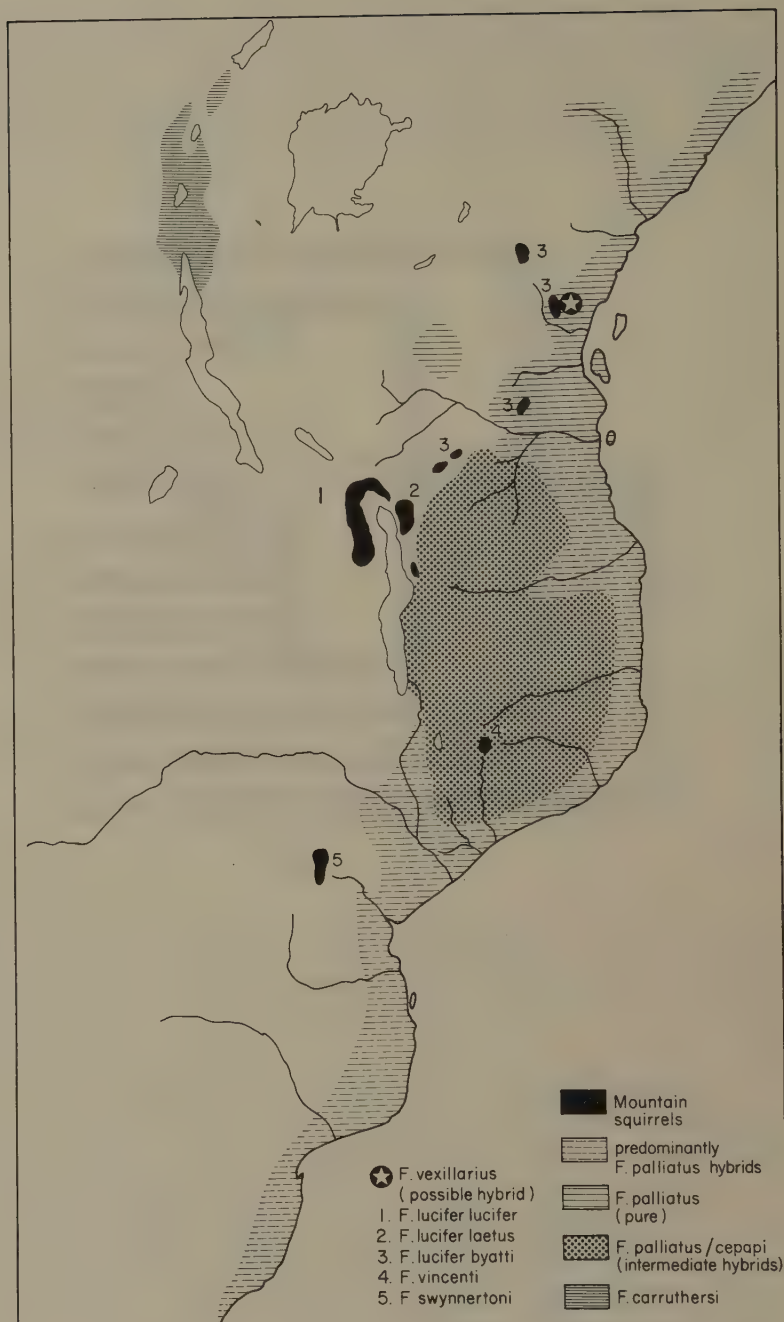
be regarded as the same species (see Ellerman *et al.*, 1953). On Namuli Mountain (2,400 m) there is *vincenti* and on Mt Selinda (2,400 m) *swynnertoni*. Both these squirrels are dark and richly coloured, indicative of long isolation in a humid environment. More important they provide a link between the typical montane squirrels and a coastal lowland species, *palliatus*. The squirrel *vincenti* is in several respects an intermediate form. It shares soft fur and four black bars on the tail with *laetus*, but the red colour which had begun to “creep” onto the scrotum, belly and inner side of the limbs of the latter race, has spread in this form all over the belly. Red bellies are most characteristic of the *palliatus* squirrel group. One southern African form, *sponsus* (see plate, p. 383) is in some respects intermediate between *vincenti* and the typical *palliatus* of the East African coast.

The geographical locus for this original “descent to the coast” was probably somewhere in the vicinity of the Limpopo and Zambezi rivers. Some of their tributaries and many lesser rivers flow from a string of scattered highlands and mountain blocks. Their forested courses would have provided short and ideal links with the coast. The sea ensures some sort of uniform and continuously moist habitat for over 3,000 km and while this strip may be narrow in places the total area of forest, woodland and moist scrub lying at sea level is very considerable. It is this habitat that *palliatus* has invaded along its entire length (see map, overleaf).

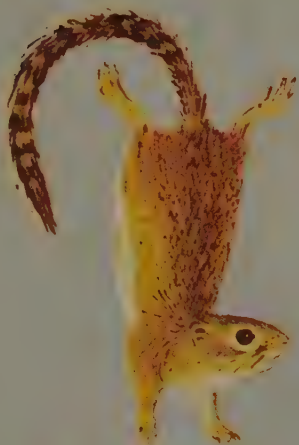
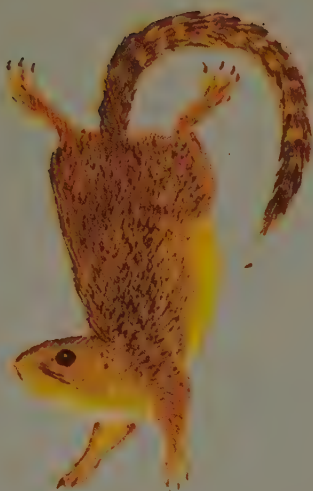
It was suggested above that the vicinity of the Limpopo and Zambezi rivers was probably the original site for this development. This area is of



A *poensis* E *vexillarius* I *p.tanae*
 B *cooperi* F *lucifer* J *vincenti*
 C *carruthersi* G *laetus* K *sponsus*
 D *byatti* H *cepapi* L *palliatus*



extraordinary interest in the taxonomy of *Funisciurus* (*Paraxerus*) as no less than fifteen forms have been described all endemic to this corner of Africa. This variety may be partly due to the development outlined above, but it is also due to the mixing of two distinct species: *F. (P.) palliatus* and *F. (P.) cepapi*, a hybridization that is possibly superimposed upon the evolution of *F. (P.) palliatus* as a distinct species. At any rate the two elements become difficult to disentangle in this region. For example, there is a squirrel in the Ngoye Hills of Zululand, *ornatus*, that is intermediate between *swynnertoni* and *sponsus*. The latter, while also a linking form, may be one of the many



grades of hybrid between an evolving *palliatus* and *cepapi*. In the profile of *cepapi* the hybrid zone is discussed and mapped and an attempt is made to define the many intermediate forms that possess to varying degrees the characteristics of the two parent stocks.

The pre-eminence of the subgenus *Paraxerus* in eastern and southern Africa and its rarity in the main forest blocks of central and western Africa is intriguing. If the group as a whole represents an older, less highly evolved stock, it is possible that less specialized squirrels are at an advantage in areas of ecological variety and subject to climatic instability.

In this sketch of an ancient radiation I am aware of having ignored some of the unique features of individual species (which have, after all, continued to evolve) in favour of an artificially linear progression. I hope to modify this over-emphasis in the profiles of the species themselves. In the face of such great taxonomic confusion I thought it worth while to attempt in this introduction to the subtribe Funisciurina a correlation between the distribution and gross ecology of the various species and the more obvious morphological trends they exhibit. One result of this exercise has been the suggestion of some sort of a genealogical position for all the known forms. Only very much more detailed study will give us a truly satisfactory picture of these remarkable evolutionary radiations.

Cuvier's Fire-footed Squirrel
(*Funisciurus*
(*Funisciurus*) *pyrrhopus*)

**Family
Order**

Sciuridae
Rodentia

**Measurements
head and body**

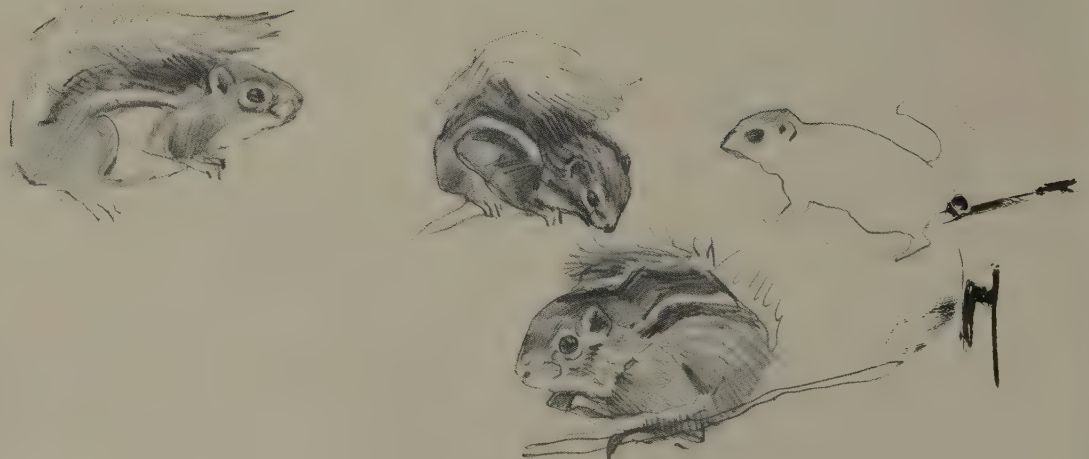
200 (135—266) mm

tail

150 (100—200) mm

weight

200 (150—250) g



Cuvier's Fire-footed Squirrel (*Funisciurus (Funisciurus)* *pyrrhopus*)

This velvety-furred squirrel has rich rufous-coloured limbs and face with a dark, almost black, back ticked with pale buff to give it a greenish brown appearance. The pale belly and throat is sharply demarkated from the dark upper side. This belly underfur is white but in many individuals from Uganda it is tinted with orange. Other variable features are the obvious presence or near absence of a pale side stripe and the intensity of red on the tail and limbs. The tail is made up of hairs of variable length, being 38—50 mm at the tip.

The tail hair bases are orange and divided by a black band from a silvery tip. The effect of this colouring is to outline the margins of the tail and its visual function becomes very obvious when the animal displays.



The taxonomy of the *Funisciurus* (*Funisciurus*) group has been the subject of recent reviews (Rosevear, 1964, 1969; Amtmann, 1966a). These texts indicate two species for Uganda, i.e.: *anerythrus* and *pyrrhopus*. The former was described by Thomas in 1890. At the time of its collection at Buguera, this village in the Semliki Valley was within Uganda, but after the boundary was redrawn, it became the Congo—hence the often repeated Uganda provenance. All recent reviews treat *anerythrus* and *pyrrhopus* as separate species, but there is disagreement about the allocation of some races to the two species, which brings into question both the validity of the species and the nature of their relationship to one another.

An examination of the British Museum skins reveals a series of beautifully graduated morphs. However their evolutionary meaning and taxonomy are obscured by the apparent sympatry of very similar forms. It is not known whether colour varies in the lifetime of individuals, nor whether there might be distinct colour phases in the same animal. Further, the ecological roles of sympatric species have not been observed and defined nor is an exact delineation of the distribution of all forms possible. It is also conceivable that some named forms are hybrids.

Of the two forms that may occur in East Africa, Allen (1927) regarded *pyrrhopus* and *anerythrus* as separate species because they occur in the same localities, but as Hopkins has remarked (unpublished manuscript)

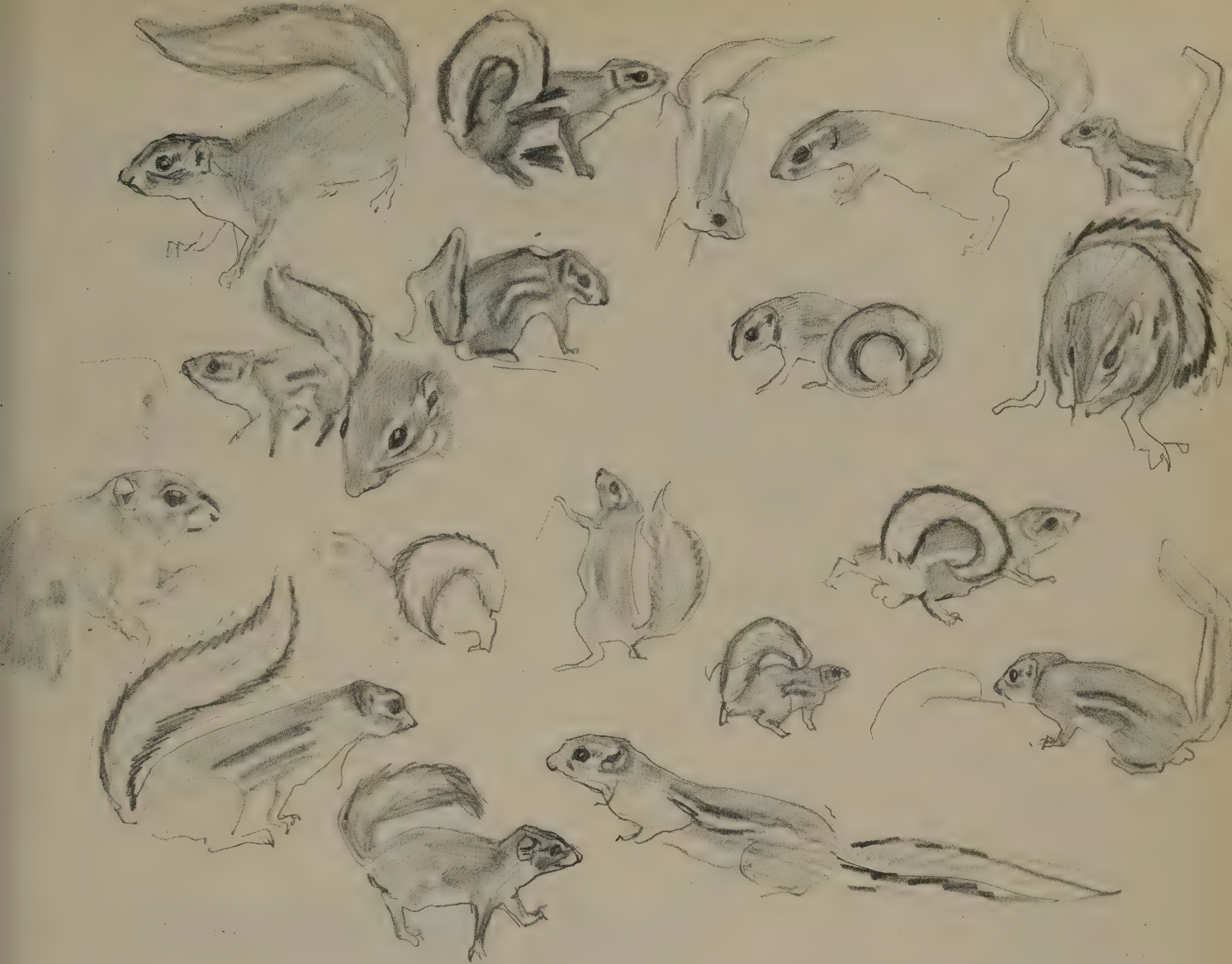
“this evidence, though conclusive that *pyrrhopus* is not a subspecies of *anerythrus*, is consistent with the two forms being colour-phases of one species, and this is perhaps the explanation of the facts. The colour-differences are that the lateral line is pale buffy in *pyrrhopus* but white in *anerythrus*, the rufous parts of the head and limbs are intense brownish rufous in the former and brown with a dull cinnamon-rufous suffusion in the latter, the underside is pure white to the base of the hairs in *pyrrhopus* (at most with a pinkish wash on the inside of the hind limbs and middle of the belly) whereas in *anerythrus* the whole of the underside is heavily washed with ochraceous and the basal third of the hairs is pale leaden grey”.

In forms that are anatomically inseparable such consistent but relatively slight differences are both a challenge and an obstacle to the understanding of the biology of this species.

Ranging through the equatorial forest belt the fire-footed squirrel occurs in most Uganda forests west of the Victoria Nile. The fire-footed squirrel is essentially an undergrowth species, found along the margins of forest streams and swampy areas generally under a closed canopy. They are common in those palmy areas that fringe water-courses within well-developed forest.

Their nests are generally made at a low level and I have found one dry leafy nest on the ground among buttress roots. Rahm and Christiansen (1963) report finding many nests, some containing gnawed kernels, built under excavated humus beneath roots and plant debris. Although some West African races are reported to make nests in the open at higher levels and in palm leaf axils, this seems to be rarer in the eastern Congo and perhaps also in Uganda.

They forage for most of their food on the ground. I collected one eating termites on the forest floor and its stomach was entirely filled with these insects. Rahm and Christiansen report red ants and other insects in the diet and also various finely chewed fruits. From other areas palm nuts, seeds, bird and



reptile eggs have been reported. Cansdale (in Rosevear, 1969) noticed they could scent insects very quickly, an unusual ability in squirrels; and although they are not very adept at catching active species like crickets, insects undoubtedly make up a high proportion of their diet. Cansdale also noticed a preference for the kernels rather than the pulp of palm nuts.

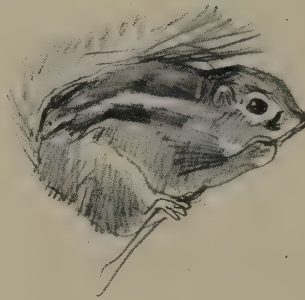
The squirrel *pyrrhopus* is a shy animal, much given to skulking in the undergrowth, and it seems to depend to a large extent upon vocal contact between individuals. It is noisy and has several distinctive calls. The most commonly heard is a succession of strident "ack-ack-ack" sounds rising and then going down the scale; this can be easily mistaken for a bird in the undergrowth. There is a similar but shorter and more emphatic call with three syllables.

While making the call, the squirrel flicks its tail and the role of the tail in communication is probably very important. When the hair is relaxed the tail is completely cryptic, the minute silver tips merely serving to break up the black. But when the hairs are parted the black hairs form a heavy outline for the red roots, and the tail can be slowly flagged up and down or curled into a sort of lop-sided circle which crowns the displayed genitalia. Both these

signals seem to be associated with sexual excitement, judging from a solitary captive male in which this behaviour coincided with a conspicuous increase in the size of the testes and anal glands. Forbes Watson who reared this animal has also observed other postures and behaviour.

These squirrels are most active in the morning and evening and are also about in both wet and fine weather. Two animals sometimes share a nest and greater numbers live and sleep together in captivity. A loose social organization interrupted by various breeding associations might be the more normal pattern.

I have collected a heavily pregnant female in Budongo towards the end of January. Cansdale (in Rosevear, 1969) reports that many young are born about October in Ghana, so it is possible that there is at least one breeding peak or season. The young are born blind and stay in the nest for some time.



Carruther's Mountain Squirrel (*Funisciurus* (*Paraxerus*) *carruthersi*)

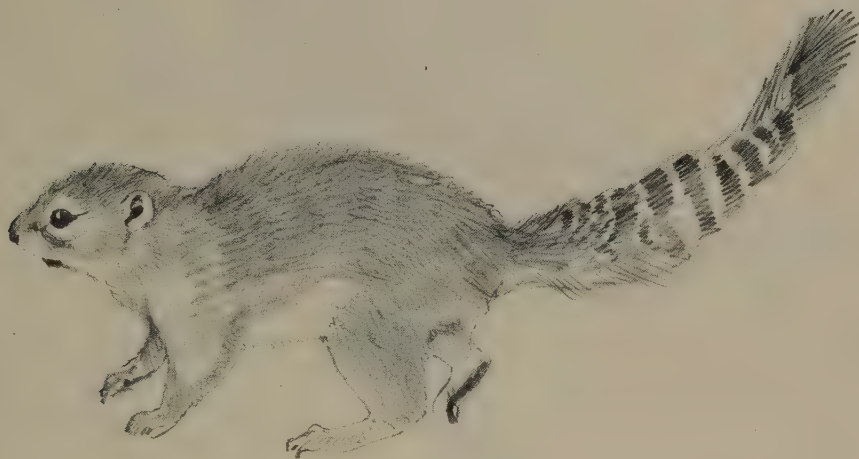
Carruther's mountain squirrel is a pretty olive-green squirrel with a cloud-grey belly and a black and yellow barred tail with a black tip. The eyes are surrounded by "spectacles" of paler cream-coloured fur. Moulting patterns sometimes cause mild contrasts to appear between the older browner fur and the new "green" fur.

This species is distributed along a chain of mountains west of Lake Tanganyika as far north as Ruwenzori; four races have been described, two of which are known from East Africa:

Funisciurus (*Paraxerus*) *carruthersi carruthersi*—Ruwenzori.

Funisciurus (*Paraxerus*) *carruthersi birungensis*—Kalinzu and Kigezi forests.

A third race, *Funisciurus* (*Paraxerus*) *carruthersi tanganyikae*, is known from the north end of Lake Tanganyika. It is possible that this race might be found on the little known Mt Kungwe, as this mountain's faunal affinities seem to link it with Burundi.



Carruther's mountain squirrel lives in forests between 1,500 m to 2,800 m and specially favours *Pygeum africanum*, a dominant tree in moist montane forests. This forest type tends to have a rather broken canopy with many trees smothered in climbers and dense tangles of undergrowth, conditions which seem to suit the mountain squirrel. This animal is certainly marvelously camouflaged on the mossy trunks of its habitat. It does not adapt well to cultivation and can only be seen in well-established forest, although it may live in stands of *Hagenia*, a high-altitude colonizing tree that regenerates in disturbed areas.



**Carruther's
Mountain Squirrel
Funisciurus (Paraxerus)
*carruthersi***

Family

Sciuridae

Order

Rodentia

Local names

Echihunaa (Lukiga), Akasendi
(Lukonjo), Ndoro (Kichagga)

**Measurements
head and body**

198—260 mm

tail

180—205 mm

weight

200—336 g

Rahm and Christiansen list the fruits of *Bridelia* sp., *Alchornea*, *Carapa grandiflora*, *Strombosia scheffleri* and a type of gourd as common foods of this species. A trace of insects has been recognized in one stomach but, since food is chewed very finely, it is virtually impossible to identify the variously coloured pulps that are generally found.

Observation is often difficult as these are very shy animals. They flee and are quickly lost in thick tangles, frequently at some height. However they seem to range through all levels of the vegetation and may come to the ground. They can be seen at any time of the day and may even be active shortly after dawn as well as in the evening.

Although occasionally in pairs they are more usually seen singly. They sometimes make a rasping, quacking call like that of the Tanganyika mountain squirrel, *F. (P.) lucifer*. The possible significance of this call was discussed in the profile of the squirrels.

They are found in the same habitat as *Heliosciurus ruwenzorii*, a species with an almost identical range but, although both squirrels can be seen close together, the latter is more exclusively arboreal.

Cassin's hawk-eagle, *Hieraaetus africanus*, which is not uncommon in the impenetrable Forest of Kigezi and Ayre's hawk-eagle, *Hieraaetus dubius*, are known to hunt squirrels. Together with genets, *Genetta*, these birds probably represent this squirrel's most important predators.

I have been unable to gather information on breeding biology but there is a record of a lactating female (with three pairs of mammae) shot in May. Bakiga hunters have told me that Carruther's mountain squirrels make large nests in liana tangles and line them with the finely shredded bark of a shrub known as "eminawa".

The affinities of this species were discussed in the introduction to the *Funisciurus* squirrels; its position in relation to the *Funisciurus* and *Paraxerus* groups lends a particular interest to learning more about its biology.

A comparison of the feeding habits of this species with those of the sympatric *Heliosciurus ruwenzorii* could give a more accurate picture of its special niche, while a comparison with the Tanganyika mountain squirrel, *F. (P.) lucifer*, might reveal the function of their peculiar molar pattern, which looks as though it might have developed in relation to a somewhat different jaw action or food preference.



Palm of left hindfoot.



Palm of right forefoot.



F. (P.) lucifer lucifer.

**Tanganyika
Mountain Squirrel
(*Funisciurus (Paraxerus)*
lucifer)**

Family Sciuridae
Order Rodentia
Local names
Sindikuleti (Kimhansa), Maleje
(Kinyakyusa)

Measurements

head and body

218—315 mm

tail 169—216 mm

weight 670—700 g

F. (P) lucifer lucifer

head and body

230—260 mm

tail 160—265 mm

F. (P) lucifer laetus

head and body

200—240 mm

tail 160—216 mm

F. (P) lucifer byatti

Tanganyika Mountain Squirrel

(*Funisciurus* (*Paraxerus*) *lucifer*)

Races

<i>Funisciurus</i> (<i>Paraxerus</i>) <i>lucifer lucifer</i>	Northern end of Lake Malawi
<i>Funisciurus</i> (<i>Paraxerus</i>) <i>lucifer laetus</i>	Mountains west of Lake Malawi
<i>Funisciurus</i> (<i>Paraxerus</i>) <i>lucifer byatti</i>	Kilimanjaro, Usambara, Uluguru, Uzungwa Mountains

The Tanganyika mountain squirrels embrace three very differently coloured races, which are scattered through numerous isolated montane forests stretching in an arc over 1,000 kilometres long.

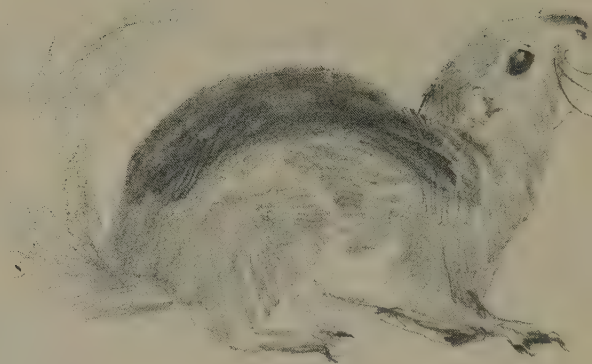
All races, however, occupy a similar high altitude niche and have much the same habits. Their skulls are also identical in structure in spite of a considerable size range. The nominate race is an extreme form; obeying Gloger's rule, its black and red colouring is probably a response to a certain measure of isolation under an extremely wet climate; the rainfall in the region in which this race is found exceeds 2,000 mm per annum. It is also possible that this colouring confers some selective advantage in relation to intraspecific signals or, more doubtfully, serves as camouflage. The latter suggestion was made by Loveridge (1933), who thought that the squirrel resembled a species of epiphyte.

F. (P.) lucifer lucifer has yellow and rufous upper parts with a black patch on the back. The tail is somewhat darker than the body with black sub-terminal bands. It is the largest form, being nearly as big as the giant squirrel *Protoxerus*.

East of Lake Malawi, the slightly smaller *laetus* also displays rich red colouring on the limbs and face, and its greenish back is suffused by a warm tinge. The tail is thickly haired, the basal half of the hairs having several dark bars on a warm ochre ground colour, topped by single broad bands of black and white. The normal, relaxed arrangement of hairs bars the tail boldly in black and white, but when the hairs are bristled, their warm grizzled bases are displayed and the tail is outlined longitudinally in black with a white halo.

F. (P.) l. byatti is a dully coloured race, known at present from Kilimanjaro, the Usambara, Uluguru and Uzungwa Mountains. Its dorsal fur is greenish but the feet are ochre and a flush of this colour also spreads up the limbs and on the sides of the face. The heavily black-barred hairs of the tail are fairly short with white tips, making for a rather dark grizzled effect but with a light haloed margin. Loveridge noticed that animals collected in the January rains were greener, while those shot two months earlier were brownish; this difference is presumably the product of a moult.

The mountain squirrels feed on vegetable matter, fruit and nuts; termites and ants are also recorded in their diet. Like many forest squirrels they seem to like sunshine, but they have been recorded as active in all weathers. Ionides (personal communication) saw them feeding on the ground at mid-day. Within their habitat they are numerous but very shy. Loveridge noticed



behavioural differences between the *byatti* squirrels living in the Uzungwa Mountains and the *laetus* squirrels in the Livingstone Mountains. The former tended to skulk at lower levels, below seven metres, and hide in thickets more or less at ground level; whilst *laetus*, like *lucifer*, escaped instead at speed into the tree tops. Behaviour must be modified according to the physical structure of the forest and to the predator with which the squirrel has to contend; circling a bough may work with one type of hawk, hiding in the undergrowth may be safer with another, while evading a genet may involve a headlong plunge into the undergrowth. It is still difficult to know just how plastic or stereotyped behaviour is in such circumstances. The cryptic colouring of *byatti* might explain its skulking; the larger size of *lucifer* and *laetus* might lead them to occupy a niche analogous to that of the giant squirrel, *Protoxerus stangeri*, which is absent from these forests.

Mountain squirrels are often noisy and their loud and distinctive call is an easy clue to their position. The possible function of this call was discussed in the profile of Squirrels. Loveridge describes this:

"its cry 'kuwhék-kuwhék' was indistinguishable from that of *byatti* at Kigogo. On February 18 I killed a pair with one shot as they were 'kuwhéking' to the accompaniment of jerking tails within six inches of one another. Another day hearing the call being repeated with regularity, I crept in the direction of the sound and approached so softly that I was within three feet of the squirrel, which was in the grass, before it saw me. It was evidently intently listening to, or approaching another animal which was calling about forty feet away. So startled was this squirrel that it dashed up the nearest tree, a bent over sapling, no thicker than a man's arm which as it was leaning in my direction, brought the animal to within six feet of, and level with my head, I covered it with my gun automatically but did not fire as it would have resulted in blowing the creature to pieces. There we stood eyeing each other, neither moving for a considerable time; finally I lowered the gun and immediately the squirrel was off like a flash, round the other side of a big tree and up to the very topmost branches far out of range. The difference in the conduct of Mahedani squirrels as contrasted with those of Kigogo was noticed many times; while the latter sought refuge in the undergrowth the Mahedani animals more usually ascended the trees".

Most mountain forests of East Africa are inhabited by the *Heliosciurus* genus of squirrels. In West Uganda *F. (P.) carruthersi* occurs together with *Heliosciurus ruwenzorii*. In like fashion the Tanganyika mountain squirrels also share their forests, but with another species, *Heliosciurus rufobrachium mutabilis*.

Little information is available on breeding: of eight female *lucifer lucifer* shot in March and April none were in breeding condition, but males with large testes have been collected in August and September. In September a single female was both pregnant and lactating at the same time. A single annual birth season is therefore unlikely, but there might be a peak in breeding activity during the drier half of the year.

In common with many other interesting forms of fauna and flora that are endemic to the tiny forest relics of Tanzania, the future of these squirrels depends upon the responsible conservation of these "islands". If the present trend of forest clearance goes unhalted, these interesting animals may be among the casualties in a widespread extinction of unique endemic species.

Swynnerton's Squirrel (*Funisciurus* (*Paraxerus*) *vexillarius*)

This squirrel is known from two specimens collected in the Usambara mountain forests around Lushoto. It is clearly related to *F. (P.) lucifer byatti*, which also occurs near Lushoto, but *vexillarius* is slightly larger, with a grey back, a tawny-orange tinted head and feet and a dramatic orange-tipped tail. The barred hairs of its tail have four black and five white, equally spaced rings, on each hair, whereas *F. (P.) lucifer byatti* has two or three black bars of very unequal spacing.

The skull is structurally identical with that of *F. (P.) lucifer* and the possibility must be kept in mind that this might be a very localized and aberrant population of *F. (P.) lucifer byatti* (it is illustrated in the colour plate, p. 383). There is yet another possibility. The Usambara Mountains are apparently the only area where *F. (P.) lucifer* and the related *F. (P.) palliatus* overlap in range, and hybridization might have occurred; *F. (P.) vexillarius* might therefore be a hybrid.

The forest in which this animal was collected is now greatly diminished and the new practice of cultivating cardamom under what is left of the forest canopy, reduces its habitat still further. Observations of this squirrel in the wild would be most interesting and might help to determine its true status.

**Swynnerton's
Squirrel**
(*Funisciurus* (*Paraxerus*)
vexillarius)

Family Sciuridae
Order Rodentia

Measurements
head and body
242 mm
tail
210 mm

Red-bellied Coast Squirrel (*Funisciurus* (*Paraxerus*) *palliatus*)

This handsome squirrel is distinguished by its strongly grizzled back and the red or orange underside and tail.

Eleven subspecies have been described but some of these seem to be the product of a long-term hybridization with *Funisciurus* (*Paraxerus*) *cepapi* which is briefly outlined in the profiles of the funisciurine squirrels.

The largest and most spectacular form is *tanae* (which is inclusive of *barawensis*). This is the most northerly population extending from the southern Somali coast to approximately the Pangani River. This race (see colour plate, p. 383) has a superficial black and white grizzle over the back, while the whole squirrel has a rich red underfur.

Between the Kenya border and the Pangani River the colouring becomes yellower and less emphatic in contrast so that the grizzled back produces a somewhat khaki effect. Animals from the northern Tanganyika coast have been named *suahelicus* but many are indistinguishable from the nominate race. A very similar form but with black feet, *frerei*, occurs on Zanzibar and Mafia.

Red-bellied Coast Squirrel (*Funisciurus* (*Paraxerus*) *palliatus*)

Family Sciuridae

Order Rodentia

Local names

Kivuki (Kiyao), Chikuvi, Kikubi
(Kimakonde), Chiruma (Kimwera)

Measurements

head and body

190—231 mm

tail 105—230 mm

F. (P) palliatus palliatus and

F. (P) palliatus frerei

head and body

216—250 mm

tail 189—270 mm

F. (P) palliatus tanae

head and body

174—200 mm

tail 115—191 mm

"*F. (P) palliatus bridgmani*"
(hybrid form)

The smaller forms described as *bridgmani* probably represent hybrids of predominantly *palliatus* facies. They occur intermittently from south of the Rufigi to southern Mozambique, interspersed with apparently "pure" *palliatus* populations. A discussion, diagram and map of the hybridization zones are included in the profile of *Funisciurus* (*Paraxerus*) *cepapi*. The evolution of the red-bellied coast squirrels from a montane stock was suggested in the profile of the *Funisciurina*. Although complicated by these two distinct

F. (P.) palliatus tanae.



developments, a detailed study of *palliatu*s would be of the greatest interest but would call for much quantitative data and field work in Mozambique, Rhodesia and South Africa.

The red-bellied coast squirrel seems to be a predominantly low-altitude form, yet it has been recorded from 1,800 m on the Milanje Plateau in Malawi and also in the Nguru and Usambara Mountains. On the latter mountains it overlaps the range of *F. (P.) lucifer byatti* and it is possible that hybridization with this species occurs (see the profile of *F. (P.) vexillarius*, p. 396). *F. (P.) palliatu*s is predominantly coastal but does extend inland in several places. These extensions of range follow major river systems in every case. For example the Milanje Plateau mentioned above is close to the Shire, a tributary of the Zambezi. In Tanzania they are recorded 600 km from the coast along the river systems draining into the low-lying depression which connects with the Great Ruaha. Other pathways inland that are followed by this species are the Kilombero, Wami and Tana rivers.

This species favours forest and thicket formations where a shaded leafy microclimate is formed at the lower levels of the forest and in thick undergrowth. At Witu, where the forest is mature and the tall trees form a canopy at 30 m superficial observations of the behaviour of the very large race, *tanae*, reminded me of *Protoxerus*.

They have been collected from holes in the baobab, *Adansonia*, and the sausage tree, *Kigelia*. One was also caught in a patch of thick bush on a coral outcrop by the sea.

Their feeding habits probably vary with the habitat; seeds, nuts and fruit forming their principal diet. They have been recorded eating the fruit of *Blighia unijugata* and the pods of *Acacia* species. They feed on fallen fruit and are often seen on the ground. Throughout most of their range they co-exist with *Heliosciurus rufobrachium* but seem to be somewhat less arboreal than that species. In favourable localities like the Gedi and Sokoke forests they are common but shy. When mildly alarmed they freeze and then, hugging the thick branches closely, skilfully creep round out of sight. Like the mountain squirrels they sometimes advertise their presence by a persistent clucking. A different call is a rather bird-like twitter. They are to be seen at various times of the day and a museum label reports one to have been caught at night.

Very often seen in pairs, their social life is probably similar to other *Funisciurus* species.

A lactating female has been collected in southern Kenya in March; another on Mafia island in October. The young are probably born in nests made in tree hollows. Nests made on open branches have not been noted.

Smith's Bush Squirrel (*Funisciurus* (*Paraxerus*) *cepapi*)

This is a medium small squirrel of grizzled sandy colouring with white belly and a moderately bushy tail, the hairs of which are marked with two black bars.* It is the typical squirrel of the southern woodland zone, occurring throughout the "miombo" and related woodlands, from Angola and northern South-west Africa in the west, to the Transvaal in the south and Tanzania in the north.

F. (P.) cepapi provides a most interesting example of hybridization on a grand scale between what appear to be very distinct species. Any consideration of its distribution is therefore inseparable from the problem of defining the nature of its interaction with *F. (P.) palliatus* in South-east Africa and this profile is largely taken up with this topic.

F. (P.) cepapi is probably derived originally from a similar stock to that of *F. (P.) ochreatus* but, while the former is distributed over a very large area of southern Africa in a relatively uniform habitat, the latter occupies a wide range of habitats in a relatively small part of tropical East Africa.

The size and appearance of *F. (P.) cepapi* varies very little over the greater part of its range, although in the dry areas near the Kalahari, animals are more grey than buff and are altogether lighter, while Tanzanian animals are darker in tone. In southeastern Africa, however, five subspecies have been described from a relatively small area. Some of these varieties are larger than the typical *F. (P.) cepapi* and are suffused with strong buff or rusty tints, particularly along the "mid-rib" of the tail. In some, the tail is marked by a third dark bar, while in others there may be two or three bars. The races are: *F. (P.) cepapi cepapi*, *F. (P.) c. cepapoides*, *F. (P.) c. bororensis*, *F. (P.) c. carpi* and *F. (P.) c. sindi*. In a species exhibiting fairly constant characteristics over most of its range, variety such as this in a limited area must be questioned. Furthermore, in this area and also over a much more extensive area to the north, the trend towards larger size and redder colouring is continued in a variety of squirrels that have generally been assigned to *Funisciurus (P.) palliatus*. These intermediate forms range over the vast territory between the

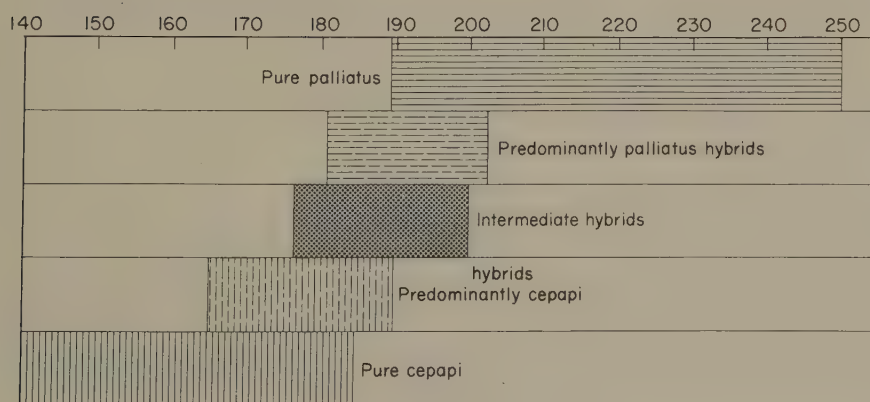
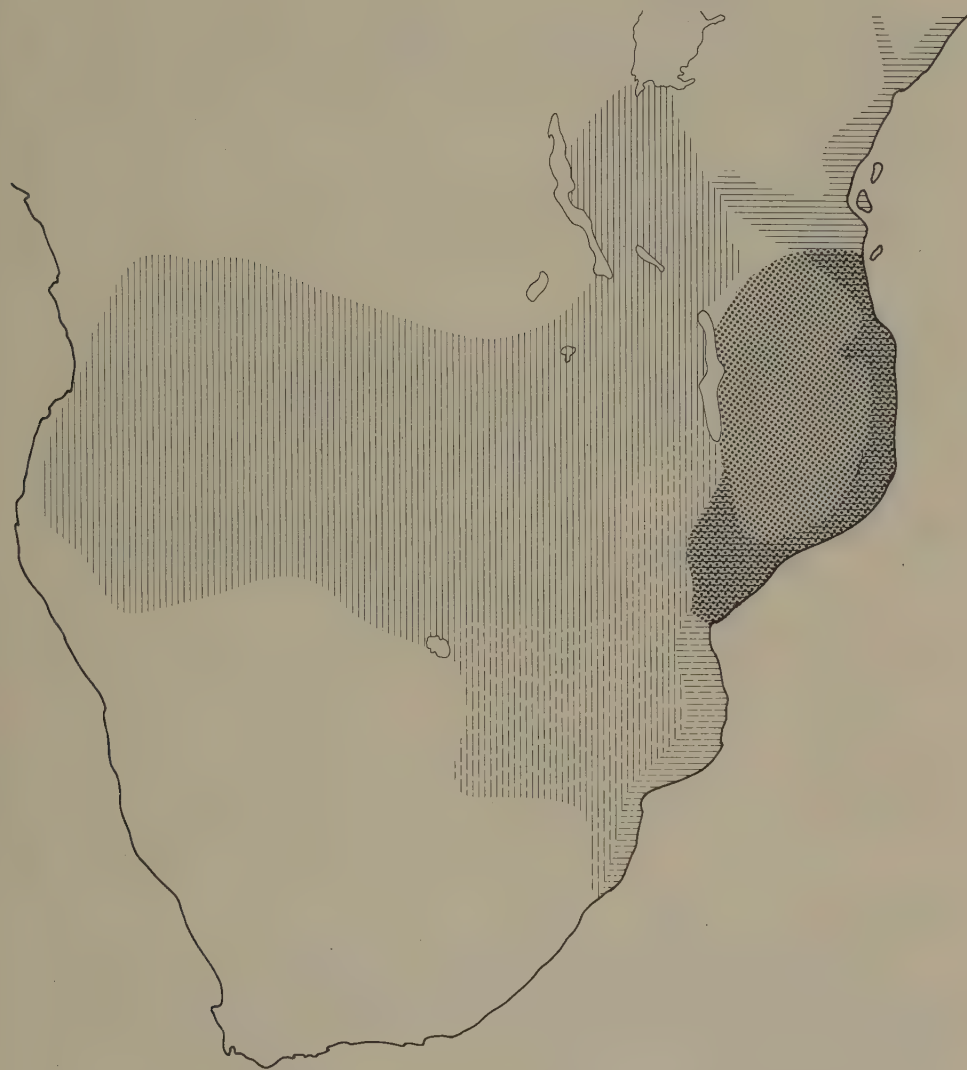
* See H in colour plate, p. 383.

**Smith's Bush
Squirrel**
(*Funisciurus* (*Paraxerus*)
cepapi)

Family Sciuridae
Order Rodentia
Local names
Kapale (Kirungu)
Mperembe (Kinyamwezi)

Measurements
head and body
145—185 mm
tail
150—180 mm
weight
250 g (approx.)

Rufigi River and Natal east of Lake Malawi. Larger and smaller types often appear to be intermingled and are scattered throughout this area, wherever there is low-lying riverine forest or coastal thicket. The occurrence of variable or unstable characteristics is a strong indication of hybridization.



The names listed below show what difficulties authors have had in assigning specific and subspecific names to animals that are almost certainly the result of an ancient hybridization.

From the lower Limpopo

Paraxerus palliatus auriventris (Amtmann, 1966b)

Paraxerus bridgemani auriventris (Roberts, 1951)

Paraxerus cepapi auriventris (Roberts, 1926, in Roberts, 1951)

From northeastern Zululand

Paraxerus palliatus tongensis (Amtmann, 1966b)

Paraxerus bridgemani tongensis (Roberts, 1951)

Paraxerus sponsus tongensis (Roberts, 1931, in Roberts, 1951; G. M. Allen, 1939)

From southern Mozambique to southern Tanzania

Paraxerus palliatus bridgemani (Swynnerton and Hayman, 1951)

Paraxerus sponsus bridgemani (G. M. Allen, 1939)

Paraxerus bridgemani (Dollman, 1914)

From southern Mozambique

Paraxerus palliatus sponsus (Amtmann, 1966b)

Paraxerus sponsus sponsus (G. M. Allen, 1939)

Funisciurus sponsus (Thomas and Wroughton, 1907—8)

Thomas and Wroughton recognized the affinities of *sponsus* in their description:

“A species intermediate in size between *cepapi* and *palliatus* with the colour pattern of the former and the bright colouring of the latter. Size rather smaller than in *palliatus*. . . . skull as in *palliatus* but decidedly smaller”.

The map (previous page) indicates the distribution of the typical *F. (P.) cepapi* and *F. (P.) palliatus*.

I have assigned to three categories the intermediate forms I have had the opportunity of examining, after evaluating several factors, namely: size, tail pattern, degree of erythristic saturation on the belly, limbs and underfur and relative proximity to one or other typical parent stock. Those that I have not seen have been tentatively assigned on the basis of published descriptions. It will be appreciated that material and information from Mozambique are scarce.

The three categories are:

hybrids of predominantly *F. (P.) palliatus* facies;

hybrids of intermediate condition;

hybrids of predominantly *F. (P.) cepapi* facies.

These categories are distinguished by three types of cross hatching and their spatial distribution can be correlated with their relative size by reference to the accompanying diagram. A comparison of this map with a vegetation map of Africa (Vol. I, p. 22) shows that *F. (P.) cepapi* or hybrids between this species and *F. (P.) palliatus* occupy the entire woodland zone of southern Africa. However, Ionides (personal communication) says that *bridgemani*

tend to stick to forest or riverine thicket, which suggests that the hybrid populations may have ecological gradients as well as size gradients. East of Lake Malawi records of typical *cepapi* seem to be very rare. There is a white-bellied *cepapi* with two bands on its tail in the Mweka Wildlife College collection which is labelled as coming from Liwalé. For the most part, however, the *cepapi* niche seems to be occupied by *F. (P.) flavivittis*.

F. (P.) cepapi flourishes in the more mixed woodland and thicket that grows on stony, hilly country and it must be either limited or encouraged by the absence or presence of tree holes in which to build its dry leaf nest. Suitable holes for their nests are not always easy to find and it is possible that the spacing of individuals is determined to a large extent by the need for shelter. Wherever annual fires are a hazard (which is over most of their habitat), this consideration must apply with force. Indeed, several observers have remarked on a local abundance of this species in particular areas and its scarcity in others. It is perhaps for this reason that stony ground, thickets and fire-resistant trees are favourite habitats. Moreover, these squirrels are reported to be especially common in the "mopane" bush of central Africa (Smithers, 1966). Here the tree species *Colophospermum mopani* dominates the vegetation and its hard, tough trunk seems to provide the right shelter for this species. I have found them sheltering in the hollows of old *Sclerocarya* trees, the fruit of which is also a favourite food. Other recorded foods are *Aloe* and *Euphorbia confinalis* leaves, the shoots of *Dactyloctenium*, the fruit of *Pterocarpus* and *Kigelia*, unspecified roots, bulbs, nuts and seeds, insects and bird's eggs.

Much of their foraging is done on the ground. They will carry food, either to store it in the home tree or to eat it in some favourite spot, usually a rock, ant-hill or trunk, where nibbled remains betray the squirrels' activity.

When an individual is disturbed within easy range of its home tree, it will generally make a dash for its hole, even across open ground. If further afield it will, instead, run up the nearest tree, keeping branches between itself and the enemy. When only mildly alarmed, it may scold in typical squirrel fashion, without hiding itself but nervously curling and twitching its tail. It is reported to mob snakes with a loud chatter.

Like most other squirrels it likes to sun-bathe, but it may be active later in the day than many other species and it is to be seen about at dusk.

Small parties of three or four animals are sometimes seen, which may consist of subadult young together with a pair. Solitary or paired animals are the most frequently seen.

The social behaviour of these animals probably resembles that of *F. (P.) ochraceus*. I have no information on breeding for East Africa.



**Ochre Bush
Squirrel,
Huet's Squirrel
(*Funisciurus (Paraxerus)*
ochraceus)**

**Family
Order
Local names**

Kinghulindi (Kiuluguru), Kahari
(Kimeru), Kassandari (Kikuyu),
Njoro (Kitaita)

Sciuridae
Rodentia

**Measurements
head and body**

138—183 mm

tail

130—187 mm

weight

93 g (one specimen).

Ochre Bush Squirrel, Huet's Squirrel (*Funisciurus* (*Paraxerus*) *ochraceus*)

Races

<i>Funisciurus</i> (<i>Paraxerus</i>) <i>ochraceus ochraceus</i>	Central and eastern Tanzania
<i>F. (P.) ochraceus aruscensis</i>	Northern Tanzania and southeastern Kenya
<i>F. (P.) ochraceus jacksoni</i>	Southern Kenya and most Kenya mountain forest
<i>F. (P.) ochraceus electus</i>	Western Kenya
<i>F. (P.) ochraceus ganqna</i>	Northern Kenya and northern Kenya coast



The overall range of this squirrel covers almost every type of woody vegetation found in East Africa. However, the rather well-defined races listed above inhabit more or less distinct geographical and ecological zones.

F. (P.) ochraceus ochraceus, which includes *salutans*, is a medium-sized race (head and body 150—175 mm) generally marked with a distinct side stripe; the belly is off white but the general colour is a sandy grizzled ochre. It occurs in thicket, *Acacia*, and *Brachystegia* woodlands and in the coastal, riverine and montane forests.

F. (P.) ochraceus aruscensis, on the other hand, is distinguished by a richer coat colour, a strong yellow underside and the lack of a stripe on the sides. Intermediate forms between *aruscensis* and the former race occur, however, over a broad area between northern and central Tanzania. Like the nominate race it ranges through various forest, thicket and woodland types.

F. (P.) ochraceus jacksoni is the largest race (head and body 160—183 mm). I have included in this race squirrels from the mountain massifs of northern Kenya, i.e.: *affinis* and *percivali* from Mt Marsabit, *animosus* from Mt Nyiro (Nyiru) and Mt Lolokwi (Ololokwe) and *kahari* from the Jombeni Mountains. These are isolated populations but they fall broadly within the range of variation of *jacksoni*. The distinguishing features are a rather greener colouring, sometimes bearing a pale flank stripe near the shoulder. Although generally darker than other races the tone of the coat is variable; as in most squirrels this is probably influenced in part by the moult and the age or condition of the individual. Altitude and humidity, however, also influence colouring, and the darkest forms come from the bamboo forest of Chania River (2,500 m) and from Embu (2,100 m). Some Mt Kenya animals also have much longer and thicker hair on the tail.

F. (P.) ochraceus electus is a paler form (head and body 138—160 mm) with a white belly, which lives in drier areas of central and western Kenya. Isolated populations of *jacksoni* type on the mountain massifs are separated by intervening areas in which *electus* is common; it is perhaps not surprising that in such a situation intermediate forms have been collected along the foothills of Mt Kenya.

F. (P.) ochraceus ganana is a small completely stripeless, pale, sandy yellow coloured squirrel (head and body 140—160 mm). It occurs in the relatively moist Witu Forest and Tana River area and also in the arid bush and scrub of the northern frontier district of Kenya. Hollister (1919) remarked that this race was closest to *aruscensis* "with which it almost certainly intergrades".

From this account of the subspecies it can be seen that the ecological range of *ochraceus* is quite exceptional for a squirrel, and it is puzzling that its geographical range should be restricted to Kenya, parts of Tanzania and the southern Sudan. Competition from closely related species, *F. (P.) cepapi* and *F. (P.) flavivittis* may keep it from expanding to the south. On the other hand, its western boundary would almost seem to coincide with the very arbitrary Kenya-Uganda frontier and no such simple explanation suggests itself. *Heliosciurus gambianus dysoni* appears to occupy a very similar niche west of Lake Rudolph but races of *H. gambianus* co-exist with *ochraceus* in other parts of the latter's range. A better understanding of this problem depends upon further information about the natural history and the ecology of

African squirrels and the interaction between species.

I have seen *F. (P.) aruscensis* living in large coffee plantations that were shaded with Australian silky oak, *Grevillea*. Sometimes they can be seen around Nairobi in garden vegetation and in *Eucalyptus* trees. Once again their adaptability is striking.

They eat buds and seeds; they also pluck flowers, eating the reservoir of nectar and discarding the petals. Roots and bulbs are dug out of sandy soil. Various fruits and berries are eaten, including the pulp of *Podocarpus* and the nuts of *Croton*. The kernel is extracted with their long, pointed tongue through a small hole nibbled in the shell. They attack unripe maize cobs on the stem and are also fond of *Acacia* gum. Several observers have suggested that they may rob birds' nests as they are often mobbed by birds. The squirrels themselves also appear to mob their enemies, flicking their tail while they scold with a high-pitched metallic burr. They pass freely from the very tops of the trees down to the ground and most races have been recorded as foraging on the ground quite frequently.

They are most active in the early morning and from the late afternoon until about an hour before dark. For the hottest period of the day they generally lie up in dense growth without returning to the home nest. They doze in dense tangles of vegetation, sitting along a branch with the tail tucked around the body.

A family of *F. (P.) ochraceus jacksoni*, transplanted from Nairobi to the shore of Lake Naivasha, live in the garden of Alan Root, to whom I am indebted for the most interesting observations on this free-ranging group. Apart from the protected nest boxes, with which they have been provided, individuals have built themselves nests in the crevices of rockpiles, a choice of shelter that is probably forced on the squirrels by the openness of the garden and a lack of holes in the dominant trees. One female attempted to build a nest in the fork of a tree, out of shredded fibres pulled off a *Eucalyptus*. It became as large as a football but fell down before it was finished.

Their social behaviour does not seem to have been greatly affected by the transplantation, except that the provision of an ample food supply and some protection from predators must increase the density and diminish the range of this little population. Pairs or groups of up to four or five individuals are not uncommon in the wild. By contrast as many as ten animals have shared the Roots' garden, ranging over an artificially small area of about half a hectare. Considering the number of individuals in wild groups there has been an interesting splitting up of the population into two groups. The natural growth of numbers as the squirrels bred seems to have led to this division. The two groups are most apparent at night, when they sleep in separate nests; during the day they share the grain at the bird table and the garden range. Although members of these groups are occasionally seen chasing each other, they have never been seen to fight. However an artificially introduced female was fiercely chased for several days and was finally killed by the others. Social tolerance within the group is such that females regularly give birth to young in nests that are shared with males and larger young.

They have been seen to be chased by augur buzzards and the little colony has been depleted by snakes and genet, the most important predators of wild squirrels. The squirrels do not wander far from the house, and without

protected nest boxes, they are not thought to stand much chance of survival in the lightly foliated and relatively open *Acacia xanthophloa* woodland.

Several observers have noticed squirrels associating with bird species, particularly the wood hoopoes, Phoeniculidae. Alan Root saw squirrels "playing with and teasing a group of wood hoopoes. The game, with first a bird, then the squirrel doing the chasing went on, back and forth, for several minutes".

There does not seem to be a breeding season as pregnant females have been collected in July and November and lactating ones in March, June, July and September. The Roots' squirrels bred throughout the year. However, there does seem to be some fluctuation in the size of the males' testes, but this seems to be an individual cycle rather than a seasonal one.

As in most squirrels, courtship is mainly taken up with a prolonged and energetic chase, which may even be initiated by the female presenting her rump momentarily to the male. The chase culminates in a brief bout of feverish grooming, mouth to mouth muzzling and often wrestling, with the animals mounting each other in turn; eventually the pair copulate. Throughout courtship the male arches his tail over his back in contrast to the more normal horizontal posture.

Litters usually consist of two or three young and Alan Root has seen two females give birth together in a hollow tree. The young do not emerge from the nest until they are three or four weeks old. After a week of hesitant exploration close to the nest's entrance, they begin to explore the branches and to play. When there are several young they may wrestle and chase each other and "solitary youngsters play with hanging flowers or strips of bark and tumble about hugging their tail and doing forward rolls" (A. Root). Females occasionally carry their young by gripping the belly, whereupon the young squirrel wraps itself around the mother's neck.

Boehm's Squirrel

(*Funisciurus* (*Paraxerus*) *boehmi*)

Races

<i>Paraxerus boehmi emini</i>	Forests of Uganda and northwestern Tanzania
<i>Paraxerus boehmi vulcanorum</i>	Montane forests in Kigezi and Ruwenzori

The two squirrel races above have been regarded by some authorities as species, for both types are thought to be sympatric at about 2,000 m on Ruwenzori. The principal difference between them is one of colour, the high altitude form having a darker, rather reddish coat, while the more widespread *P. b. emini* has a paler and more greenish colour. This ground colour is made up by the individual hairs having a grey base, a yellow shaft with fine shiny black tips. *P. b. vulcanorum* has a dark grey underfur with an altogether redder tinge and darker tone. However, the proportions and visual impact of the black stripes are rather different in the two forms, *P. b. emini* having a pale yellow mid dorsal stripe and an almost white stripe separating the two broad black bands on each side. In contrast *P. b. vulcanorum* has a broad greenish russet band in the mid dorsal line, flanked by black bands and a yellowish instead of white stripe, below which a very narrow black stripe separates it

Boehm's Squirrel (*Funisciurus* (*Paraxerus*) *boehmi*)

Family Sciuridae
Order Rodentia
Local names
Echihunaa (Lukiga), Betu
(Kuamba)

Measurements head and body

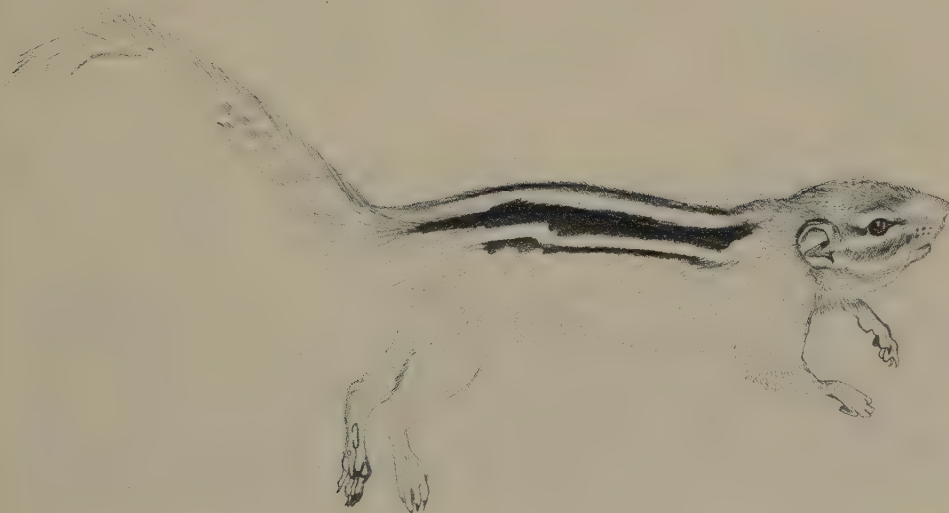
100—152 mm

tail

90—200 mm

weight

40—101 g



from the grizzled ground colour (see drawing). This change of emphasis suggests that some differentiation has taken place between these populations in addition to a general darkening and erythrism, which could be attributed to altitude alone. The question of sympatry on Ruwenzori would be worthy of further investigation.

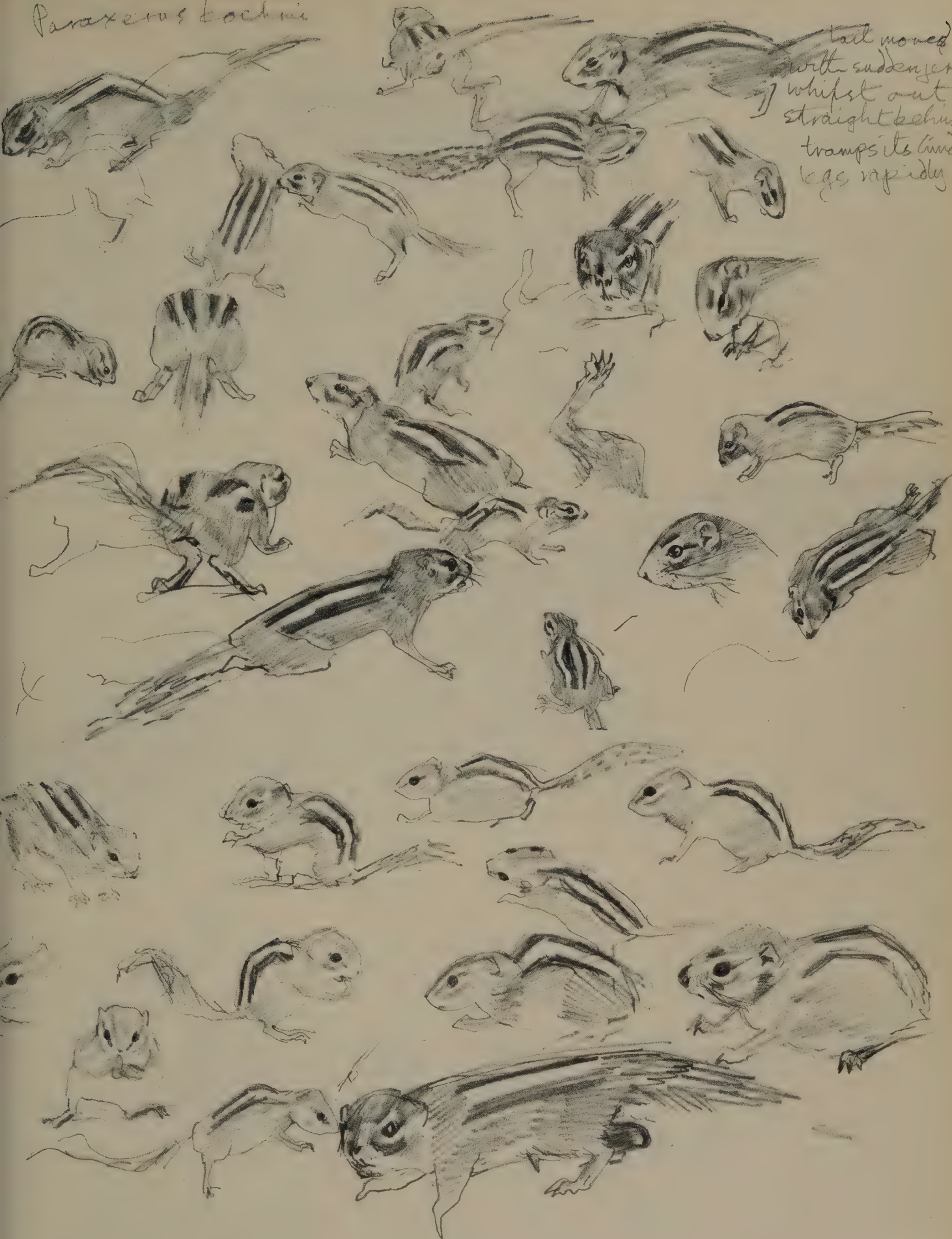
Boehm's squirrel ranges throughout the Central Forest Refuge and down the eastern Congo as far as northern Zambia and Malawi. The relict forests of the southern Sudan, the Uganda forests west of the Nile and those of western Tanzania provide its most easterly habitat. This is primarily a true forest squirrel, although Rahm and Christiansen (1963) report it from wooded



savanna in the Congo. It is common in *Cynometra*, mixed, lowland, swamp and montane forests, extending up to about 2,300 m. It is typically found in the undergrowth and lower storeys of the forest, being particularly fond of thick tangles of lianas. It seeks much of its food on tree trunks and branches and also on the ground. Its principal food is insects. Of thirty stomachs investigated seven contained insects alone (mainly ants but also caterpillars and beetles), a further ten contained a large proportion of insects, whilst eight had

Paraxerus boehmi

tail moved
with sudden jerks
whipst out
straight behind
tramps its hind
legs rapidly



insect traces. Of the thirty stomachs, twelve contained vegetable matter (including the fruit of *Rubus* and epiphytic mushrooms) and ten contained large quantities of tree resin. Rahm and Christiansen (1963) saw a squirrel carrying a piece of the cucumber-like *Shaerosicyos sphaericus* and also identified the resin of the *Albizzia* tree in stomach contents.

In its search for food the squirrel explores the branches with its mouth, tearing away moss, lichen and bark. Occasionally little bits of the moss and lichen are eaten, probably accidentally. Sometimes it feeds as it descends vertical trunks or hangs from beneath a horizontal branch. I have seen a small brown flycatcher-like bird chivvy one of these squirrels by aggressive dive-bombing until it ran away. Whether this indicates any propensity to rob nests is uncertain. Boehm's squirrel itself makes a very bird-like chitter which apparently denotes mild alarm. This display is enhanced by up and down flicks of the tail. This squirrel exploits a habitat which is dominated by birds and it is subject to very similar hazards, so there may be some advantage in sharing similar alarm calls. If competition plays any role at all this is just as likely to come from birds as mammals. I have seen flocks of wood hoopoes, *Phoeniculus bollei*, examining and probing bark and epiphytic growth which had recently been rather more thoroughly examined by a pair of Boehm's squirrels.

Their nests are also rather like those of some birds, being dense agglomerations of fine twigs and grasses with a chamber in the middle lined with finer materials, including strands of soft shredded bark. These nests are built within thick tangles of vegetation two to eight metres from the ground. Rahm and Christiansen report finding a nest in the liana *Cyathula uncinulata*.

Courtship resembles that of other squirrels in being taken up by a long chase. Copulation is achieved even while hanging on a vertical trunk. Pregnancies have been recorded for January (one), June (one), November (one) and December (one), while lactating females are recorded for January (one), May (two), June (one) and July (one). Non-breeding females are recorded for the same months so that if there is a breeding season in the dry weather of December to January, it is a peak in reproductive activity rather than an exclusive season. Some breeding activity probably occurs throughout the year.



Alexander's Dwarf Squirrel (*Funisciurus* (*Paraxerus*) *alexandri*)

This very small greenish squirrel is easily distinguished by its white ears, whilst its back is marked by a medial tawny yellow stripe flanked by a dark line and a thin white line. The tail is long and thinly haired.

Allen (1927) noticed that animals collected in the eastern Congo between November and February had very much more definition to their colour and pattern than those collected in April, May and October. Loveridge (1942) thought this to be probably two distinct seasonal pelages rather than fading due to wear. A similar phenomenon has been observed in the oriental squirrel *Tamias*.



**Alexander's Dwarf
Squirrel**
***Funisciurus* (*Paraxerus*)
*alexandri***

Family Sciuridae
Order Rodentia
Local names
Kagbetu (Lubwizi)

Measurements
head and body
90—120 mm
tail
110—144 mm
weight
37—72 g

This dwarf squirrel has a very limited distribution from the northeastern Congo to the Victoria Nile. It is a lowland forest species not found above 1,500 m, being relatively common in *Cynometra* forest and most types of lowland rain forest within its range. It is commonly seen moving in methodical fits and starts over the surface of boles and branches of very large forest trees such as mahogany *Khaya*, ironwood *Cynometra* and mututu *Klainedoxa*.



This searching is probably mainly for insects; all stomachs investigated tend to contain equal quantities of ants and finely ground vegetable matter with occasionally some tree resin as well.

This species therefore resembles the slightly larger *F. (P.) boehmi* both in habitat and diet and although this species has a much more restricted range, both in area and altitude, the two animals can sometimes be seen at the same time in some Uganda forests.

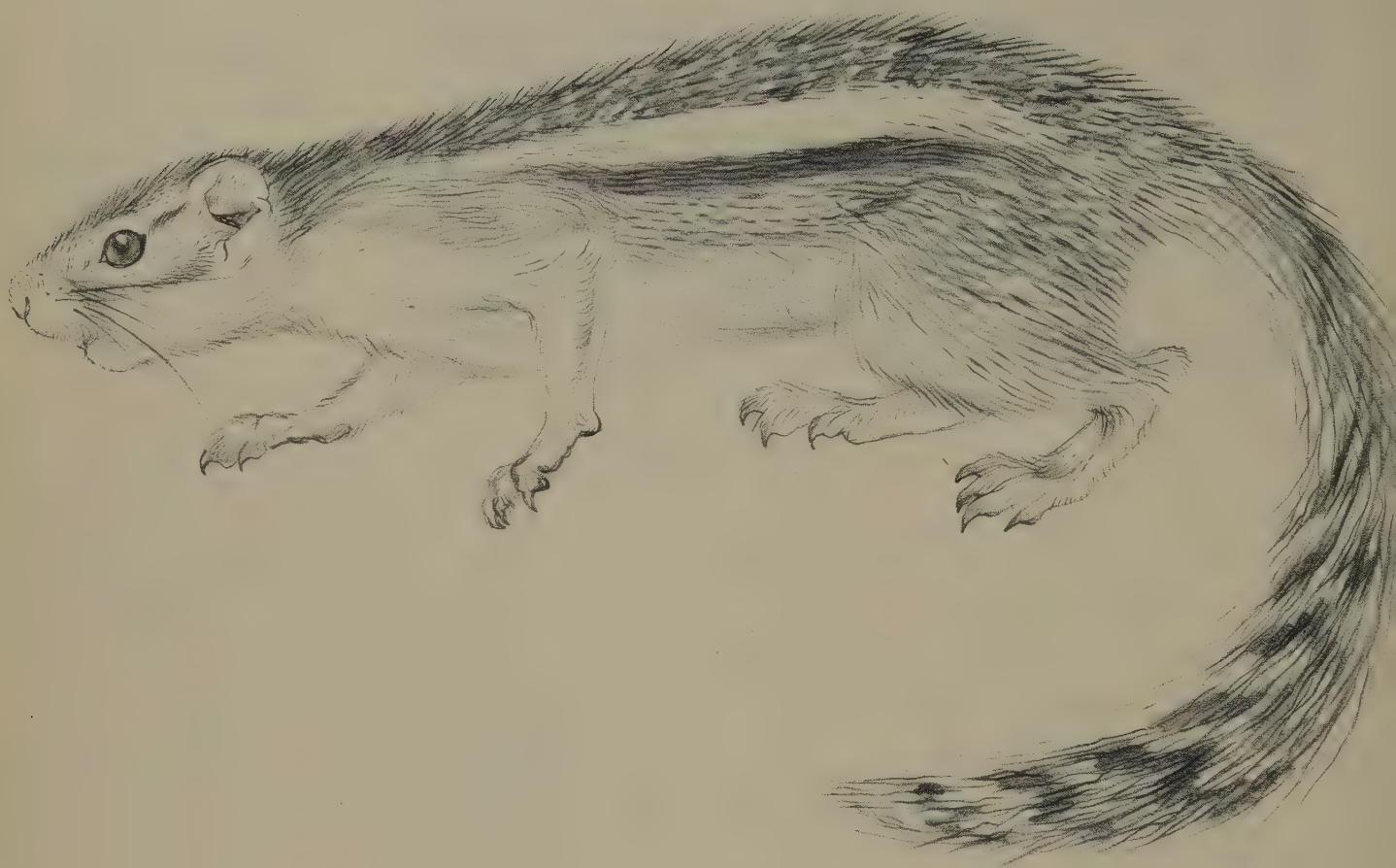
Alexander's squirrel is perhaps more ready to ascend into the canopy but it is unlikely that its smaller size is related to the use of the smaller twigs and branches. It is more likely that this animal exploits the micro-fauna and perhaps the micro-flora of the massive trunks and branches of well-developed

lowland forest trees. It does seem to be less dependent on lianas and tangles than *F. (P.) boehmi* and I have seen a *F. (P.) alexandri* apparently using a hollow branch as its home. This hole was high up but below the closed canopy of *Cynometra* forest where there was very light spindly undergrowth and virtually no liana growth. It is not known whether this species builds nests like *P. boehmi*.

This species can be seen about at any time of the day and it is usually either solitary or in pairs.

There is little information about breeding; Rahm found a pregnant female in the eastern Congo in September, a Bwamba female was pregnant in November. The testes seem to vary in size, whether this follows a seasonal cycle or an individual cycle independent of the seasons remains to be seen. Juveniles have been collected in April, October and November.





**Striped
Bush-squirrel**
(**Funisciurus (Paraxerus)**
flavivittis)

Family Sciuridae
Order Rodentia
Local names
Lileje (Kiyao), Uhindi (Makonde)

Measurements
head and body

165—193 mm

tail

141—175 mm

Striped Bush-squirrel (*Funisciurus* (*Paraxerus*) *flavivittis*)

Races

<i>Funisciurus</i> (<i>Paraxerus</i>) <i>flavivittis</i> <i>exgeanus</i>	Southern Tanzania
<i>Funisciurus</i> (<i>Paraxerus</i>) <i>flavivittis</i> <i>ibeanus</i>	Northeastern Tanzania and southeastern Kenya

This is a medium small, grizzled squirrel whose most distinctive mark is a white stripe down the side, the visual impact of which is emphasized by dark coloured stripes above and below. There are less conspicuous lines on the face. Several races have been described but these may be false distinctions as variations in colour may be due as much to individual cyclic moulting and to the fur's age as to any consistent difference between different populations. Hinton (1920) first pointed out that changes in colouring probably depended on the physiological condition of the individual rather than on a seasonal factor.

Of a series of southern Tanzanian animals collected in July, four showed moult patterns while others showed no sign of moulting. Captive squirrels of several species have also been noticed to undergo considerable changes in colour.

This species probably shares a common origin with *F. (P.) ochraceus* and *F. (P.) boehmi*. If Portman's thesis is correct, that striped patterns taking no account of the body and without accentuation of the head are "indicative of low rank" (Portman, 1952), is it possible that striped squirrels (which also occur in America and Eurasia) are particularly primitive? Or is this pattern a response to special needs in some small squirrel niches, with different squirrels converging without any phylogenetic implications? If this squirrel is in any way primitive could its peculiar distribution be regarded as a relict range? The unusual features of its distribution are that between the Rufigi and Rovuma rivers it is a common and widespread species occupying a variety of habitats. North of the Rufigi it is very much rarer and it is in this zone that it is apparently sympatric with a comparable species of squirrel, *F. (P.) ochraceus*. I have no information on the status of *F. (P.) flavivittis* in Mozambique but it is not known from the southern areas of this country, where there are instead squirrels belonging to the *F. (P.) cepapi* facies which also appears to occupy a broadly comparable niche. These two squirrels are dominant over very large areas to the north, south and west of *F. (P.) flavivittis* and it looks as though the latter might be competitively inferior to these species. Its range may actually be contracting, in which case it might have been more widespread in the past and *F. (P.) ochraceus* and *F. (P.) cepapi* could therefore represent more recently evolved species.

In the southern region of Tanzania they are common in both savanna, forest and cultivated land. They have been noticed to favour *Uapaca* bush, where they probably feed on the fruit. They nest in the holes and hollows of hardwood trees and Ionides even found them living in the roofs of houses. One has been seen in a solitary tree growing on an isolated rocky outcrop.



They probably feed on much the same foods as *P. cepapi*; fruits, seeds, buds, leaves and roots with some animal matter making up most of the diet. They will also steal millet and other grain from the fields. The squirrels feed on the ground as well as in trees.

In behaviour, escape responses may be simply hiding on the other side of a branch or flattening the body and keeping still, or they may flee for their hole if it is nearby. They are commonly to be seen basking near their holes in the early morning sunshine. Pairs or females with young are often seen together; larger associations have not been recorded. In areas where there are many old hardwood trees they are noticeably more numerous. An abundance of secure natural shelters is probably the main explanation for this increased population density. They are safe from both predators and fire in the crevices and hollows of these trees. In fact, Loveridge (1942) remarks that these holes deter the millet farmers from revenging themselves on these little grain thieves.

Very small squirrels have been collected in March and April and half-grown young in June. During April Loveridge collected thirteen males to only four females, one of which was with its single young, and he suggested that there may be a birth season at this time. If this is so, there may also be a second season as young have been recorded in September.

One or two young have been recorded as born in nests made inside hollow trees. Loveridge described a nest made from a large assemblage of coconut fibre with some grass. The piercing squeaks of the young when disturbed attracted the mother, but she fled after an initial approach.

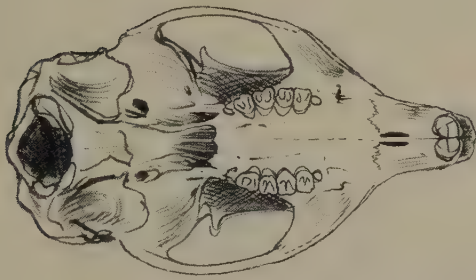


Sun Squirrels and Giant Squirrels

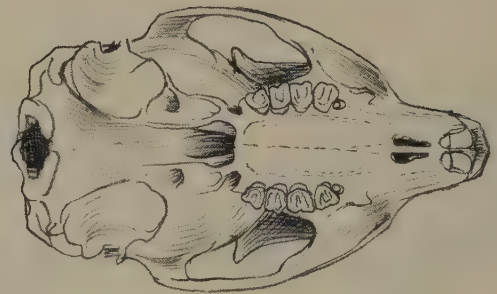
Protoxerini

This exclusively African group of squirrels is most closely related to the funisciurine squirrels and must have evolved on this continent. A glance at the taxonomic history of some of the species of the *Funisciurus* (*Paraxerus*) group shows how many authors judged some of them to be *Heliosciurus*. One species *H. ruwenzorii* even has the same tooth count and might prove to be a linking form.

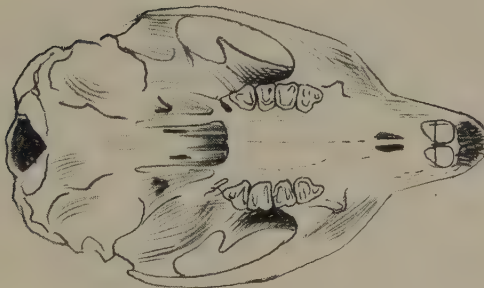
The giant squirrel *Protoxerus* and the West African *Epixerus* are probably the most fully evolved forms. They are limited to the high forest zone.



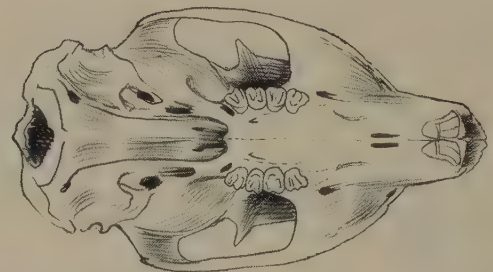
F. (P.) lucifer byatti.



H. ruwenzorii.



H. rufobrachium.



P. stangeri.

Sun Squirrels (*Heliosciurus*)

The sun squirrels are restricted to the African tropics and have been grouped with the giant squirrels, *Protoxerus* and *Epixerus*, in the tribe Protoxerini (Moore, 1959).

There are three species. *Heliosciurus ruwenzorii* is a montane squirrel of restricted distribution. *H. rufobrachium* is a common and successful species of lowland and montane forests with a range across tropical Africa. *Heliosciurus gambianus* ranges from the Ethiopian Highlands across the Sudanic savannas and woodlands with some populations in Angola, the Congo (Zaire), Zambia and western Tanzania.

The very numerous races of sun squirrels deserve special attention as they may assist our understanding of two important factors in the speciation of African mammals. The nature of the interaction between forest and savanna habitats is evidently one central problem in the natural history of sun squirrels. The other is the role of highlands in eastern Africa as isolators of populations.



Apart from the general but not exclusive preference for drier habitats, *H. gambianus* is conveniently distinguished from *H. rufobrachium* on the basis of size. The two species clearly belong to a single complex, but they are sympatric in several localities and the criterion of size has proved to be one of the useful means of distinguishing them (Rósevear, 1963). However the requirements of an identification key may very well obscure the further understanding of a very big complex of populations; 22 races of *rufobrachium* and 24 of *gambianus* are described in Amtmann's 1966b review. The cleavage between species on the criterion of size divides two very similar forms. *H. g. multicolor*, for instance, appears to be a smaller Ethiopian isolate of the Mt Kenya montane squirrel, *H. r. keniae*, so similar are they in appearance and colouring. Six races of *H. gambianus* have been described from Ethiopia, and this broken mountainous area might have provided conditions suited to the speciation of these squirrels, some of which are dark forms with white flashes on the throat and chest.*

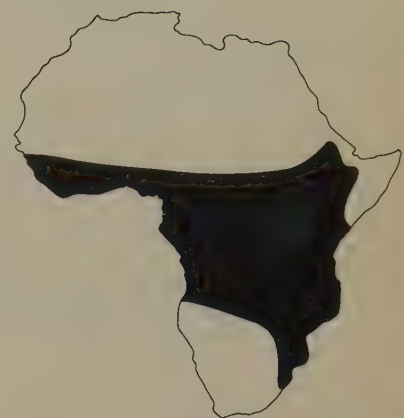
As I suggested in Volume I (pp. 73 and 313), the highlands in northeastern Africa may have had a special evolutionary significance for the interaction of forest and savanna faunas. They have probably been subject to climatic fluctuations that would at first have isolated and then degraded the forests, forcing those animal populations that survived these vicissitudes to adapt to a drier regime. Invasion of the savanna by forest or montane forms would thus be made possible in those rare populations that made a suitable "genetic reconstruction and ecological transformation" (Mayr, 1963). It is conceivable that some such situation applies here to the sun squirrels.

In this context the gross distribution and interaction of the two main species is of great interest. *H. rufobrachium* occupies a predominantly forest environment, extending as far as East Africa, where it often lives in relatively dry habitats. Perhaps this betrays more humid climates in this area in the past but it might also reflect an antecedent position for *rufobrachium* which therefore excluded or blocked the entry of *gambianus*. The presence of the latter in the forests of the Congo basin implies instead that it established itself in this area during an arid phase and has maintained itself in spite of the recent return of forest. The maps opposite show a hypothetical sequence of events that might explain the evolution and peculiar distribution of these sun squirrels.

The fragmented distribution pattern of *rufobrachium* in eastern Africa suggests that they once ranged right across the tropics of Africa; probably during a relatively recent period of extensively wet conditions. Desiccation followed accompanied by a *Heliosciurus* population adapting to drier habitats. At the height of the dry period this population (*H. gambianus*) expanded and found its way through a corridor in the Congo basin into the southern savannas, where it may be still expanding its range.

The contrast between large areas of mutual exclusion, and several restricted localities where they are sympatric, would make the study of the latter regions well worth while. Mt Elgon is the principal East African site where the species are sympatric.

* This colouring resembles that of *H. ruwenzorii* rather closely, however none of these Ethiopian squirrels have the vestigial premolar that distinguishes *H. ruwenzorii* (which may be a relic species).



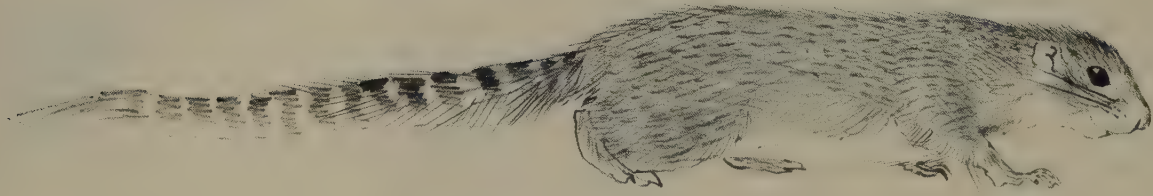
Evolution of *Heliosciurus*
Ancestral *rufobrachium* in wet period



Ancestral *rufobrachium* in arid period



Invasion of drier habitats by *H. gambianus*



Forefeet with open and closed palm.

**Ruwenzori Sun
Squirrel
(*Heliosciurus
ruwenzorii*)**

Family
Order

Sciuridae
Rodentia

Local names

Echihunaa (Lukiga),
Akasendi (Lukonjo)

Measurements
head and body

200—252 mm

tail

225—272 mm

weight

205—377 g

Ruwenzori Sun Squirrel (*Heliosciurus ruwenzorii*)

Races

<i>Heliosciurus ruwenzorii ruwenzorii</i>	Ruwenzori Mountains
<i>Heliosciurus ruwenzorii schoutedeni</i>	Kigezi

This squirrel has thick, dense fur of a grizzled dark grey. The relatively slender tail is boldly cross-barred. A warm tawny tint appears on the limbs and round the mouth. There is a broad white stripe running down the underside from throat to genitals. But for the possession of a vestigial extra premolar in the upper jaw, this animal would probably be regarded as a race of *H. rufobrachium*, for an extraordinary similarity of colouring exists between this species and *H. r. kenya*e and also some smaller *Heliosciurus gambianus* from Hora-daka, Arussi and Didessa in Ethiopia. All these squirrels are dark montane forms, with a white flash on the underside, but *H. ruwenzorii*'s restriction to the mountains of the Central Refuge and its vestigial tooth suggest that it might represent some sort of a relict population possibly linking *Heliosciurus* with the funisciurine squirrels.

The Ruwenzori sun squirrel inhabits forests between 1,600 m and 2,700 m in the eastern Congo, western Uganda, Ruanda and Burundi.

It seems to flourish both in well-developed forest and in the very degenerate conditions that accompany cultivation. It has taken readily to crop raiding, feeding on such exotic foods as guavas, paw-paw, bananas, millet and palm nuts. Under more natural conditions its food includes the fruits of *Parinari*, a dominant tree in some areas, *Syzygium*, *Conopharyngia*, *Carapa* and also the berries of *Strombosia*. Some plant stems are eaten whilst insects and *Usnea* lichen have also been recorded in stomachs.

They are reported to store nuts in caches and they make grass and leaf nests. According to Mukiga observers they favour "eminawa" and "emirandagasi" trees.

Most active during the morning and afternoon, they are generally more conspicuous than Carruther's mountain squirrel, *F. (P.) carruthersi*. They carry the tail behind in the line of the body and flick it very much less frequently. Usually seen in pairs or as solitary animals, their behaviour is little known.

Rahm and Christiansen (1963) found three young ones in March in a nest made in the thatch of a hut, and collected a pregnant female in February, suggesting that there might be a birth season or peak at about this time.



**Gambian Sun
Squirrel
(*Heliosciurus
gambianus*)**

Family

Sciuridae

Order

Rodentia

Local names

Ngilesia, Eles (Karamojong), Ilesia
(Ateso), Beryenyet (Kisebei)

**Measurements
head and body**

174—210 mm

tail

185—218 mm

weight

250—340 g

Gambian Sun Squirrel (*Heliosciurus gambianus*)

Races

<i>Heliosciurus gambianus elegans</i>	North Uganda and northwest Kenya
<i>Heliosciurus gambianus lateris</i>	West Nile
<i>Heliosciurus gambianus rhodesiae</i>	West Tanzania

This species is represented in West Kenya and North Uganda by the race *elegans*, a greyish-brown squirrel with a grey-white belly. The rump and base of the tail have an orange tinge. In the driest areas west of Lake Rudolph they become somewhat paler in tone, a variety known as *dysoni*. In West Nile the race *lateris* occurs. The total range of *rhodesiae* in West Tanzania awaits definition. The species as a whole ranges from Ethiopia to Senegal, mostly in



the better wooded savannas, it also occurs in forest south of the Congo River in Angola and part of Zambia. Other populations live within the forest belt in Liberia and the Cameroons, where they are sympatric with *Heliosciurus rufo-brachium*, a situation which also occurs on Mt Elgon.

A very wide range of vegetation types is inhabited by this species. In East Africa it lives in well-wooded localities such as water courses and thickets on rocky outcrops even in the very dry areas west of Lake Rudolph. It is common in Karamoja and Teso but scarce in Tanzania.

The Gambian sun squirrel feeds on fruits, seeds and the pods of *Acacia* species. In captivity it will eat exotic fruits such as avocado and paw-paw. Insects, eggs and young birds are also recorded in its diet. It descends to the ground to pass from tree to tree, and although limited mostly to low scrub it seems to prefer feeding and moving about on the branches.

Individual sun squirrels are very tame and bold and often scold passers-by with a loud repetitive churring noise. They also make a high-pitched noise with a lower bark interposed from time to time, possibly signifying mild alarm. According to Cansdale (Rosevear, 1969) they become active relatively late and retire early. He also noted that the young had a plaintive but musical call. Watson (1950) described the courting female making a harsh grating squeak. Breeding seasons are not known but young ones have been collected from Karamoja in February.



**Red Legged Sun
Squirrel**
**(*Heliosciurus*
rufobrachium)**

Family

Sciuridae

Order

Rodentia

Local names

Kalerebwe (Luganda), Nkenda
(Kisambaa), Gerurut (Masai),
Kwereru (Kisebei), Kau (Gisu),
Emuna (Lubukusu), Orosh (Kitaita),
Shindi (Kisagalla), Kapali (Kirungu),
Kiperemendo (Kikinga),
Imbelemende (Kinyakyusa),
Imbelembe (Kinyika),
Kipare (Kuamba)

Measurements
head and body

200—254 mm

tail

210—300 mm

weight

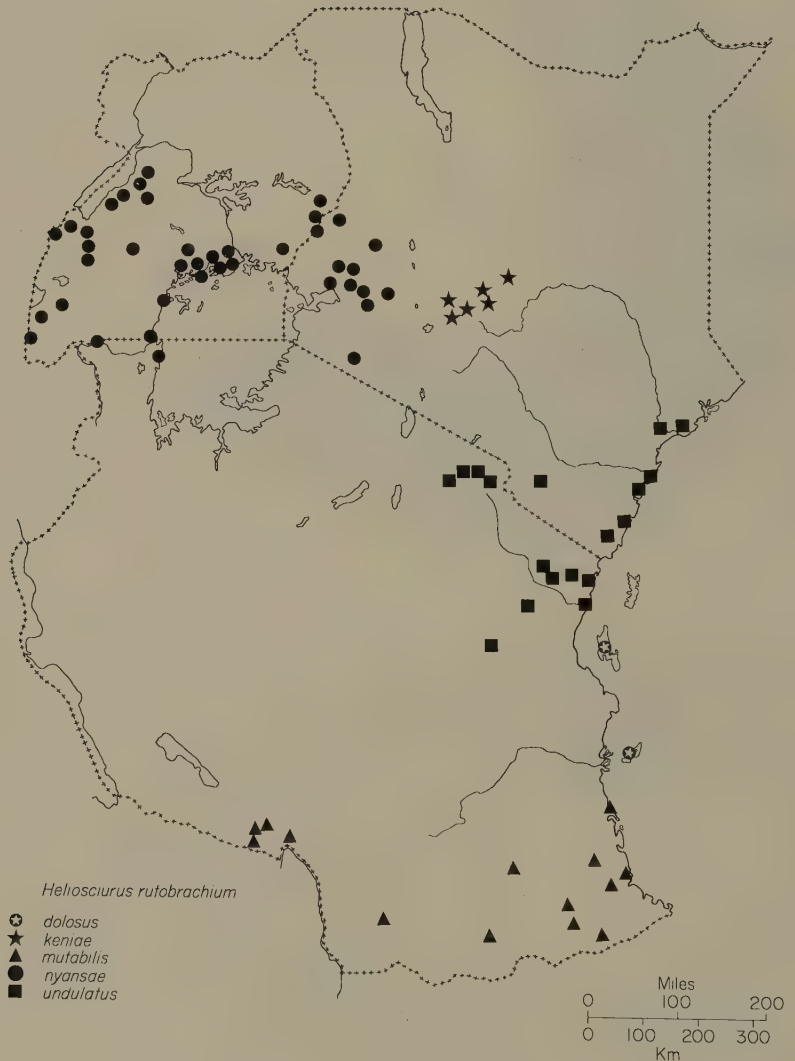
250—403 g

Red Legged Sun Squirrel (*Heliosciurus rufobrachium*)

Races

<i>Heliosciurus rufobrachium dolosus</i>	Mafia and Zanzibar islands
<i>Heliosciurus rufobrachium keniae</i>	Mt Kenya and Aberdare Mountains
<i>Heliosciurus rufobrachium mutabilis</i>	Southern and southwestern Tanzania
<i>Heliosciurus rufobrachium nyansae</i>	Uganda, northwest Tanzania and western Kenya
<i>Heliosciurus rufobrachium undulatus</i>	Northern Tanzania and eastern Kenya

The colouring of the red legged sun squirrel seems to be responsive to the ecological conditions under which a population lives. Thus the squirrels of



the more humid areas of Uganda and Mt Kenya, *nyansae* and *keniae*, are rather dark; those of the drier areas, *mutabilis* and *undulatus*, are very much paler; and not all forms can really be said to be red legged, although the widespread *nyansae* race is certainly well marked with red or orange on the limbs. Their altitudinal range is very great and they are known to range to the top of the forested zones on Mt Elgon and Mt Kenya.

Red legged sun squirrels occur in forested or heavily wooded areas, from Senegal to the southern Sudan and Kenya, and then south to Mozambique. They seem to be rare in the forests south of the Congo. Possibly *Heliosciurus gambianus* is a direct competitor in this area. Perhaps, like the elephant shrew, *Petrodromus tetradactylus tordayi*, *H. gambianus* might have maintained its supremacy in this area from an earlier period of greater desiccation (see Vol. I, p. 66). Most of the areas in Tanzania and Mozambique where *H. rufobrachium* occurs are thought not to have carried true forest for a very long period of time. Yet on the criterion of habitat most of this region should be the home of *gambianus* and not *rufobrachium*. Perhaps during the critical stages of adaptation, *rufobrachium* was free from the pressure of a competitor that was already pre-adapted to seize the opportunities offered by changes in climate and vegetation. However, in spite of holding its own in southern and eastern Tanzania, it is replaced by *gambianus* in the woodlands of western Tanzania.

Red legged sun squirrels are most abundant in secondary growth, along streams and rivers, swamps and forest edges. They tend to move about at medium heights, although they move from the lowest levels to the canopy with rapidity and ease. Southern and Hook (1963) saw one build a twig nest in the canopy after collecting and carrying the building materials from the shrub layer. Nests may also be made in holes in boughs or trunks, in hollow logs or even in beehives. The latter nesting site is not uncommon in the "miombo" woodlands of southern Tanzania, and the squirrels are said to nest successfully irrespective of whether the hives are occupied or not. They are also known to have nested in thatched roofs.

Feeding is mostly accomplished in trees, but being opportunistic feeders, they sometimes descend to the ground when there is an attraction below. I have often had my attention drawn to these squirrels as they cracked open seed pods in the canopy, several animals feeding in the same tree at one time. Leaves, buds, both fresh and dried fruits, nuts, including those of *Elaeis* and *Phoenix* palms are common foods. At Witu a sun squirrel was feeding with *F. (P.) palliatus* on the ripe fruits of *Blighia unijugata*. Ansell (1960a) has recorded *H. r. mutabilis* eating *Kigelia* fruit and the leaves of ivy, an introduced plant. Insects are eaten and one animal from southern Tanzania had filled its stomach exclusively with grasshoppers during the early rains. Eggs, small birds and even geckos are occasionally included in their diet. Cansdale kept this species in captivity and reported that they fought over food (Rosevear, 1969).

They are often rather tame squirrels and will sometimes scold in a similar way to *H. gambianus*, clucking at the intruder. They also make a ringing metallic note while flicking the tail, which is probably the specific contact or mating call. If frightened they tend to flee through the branches in a fast but conspicuous rush from tree to tree, often gaining height as they go. They sometimes sun-bathe on exposed trunks and are most active in the middle of

the morning and in the late afternoon. They are possibly more vulnerable to hawks than some of the timid, cryptic squirrels. On casual assessment they appear to be commoner, and expose themselves more than other genera; perhaps their more numerous young are a response to heavier predation.

Verheyen and Verschuren (1966) repeated trappers' claims that these squirrels kill snakes, one killing and subsequently eating morsels of a four-metre long python. It may be that this story is the result of a confusion between the arboreal mongoose, *Herpestes (Myonax)*, and the squirrel, as many tribes have one name for both animals.

Verheyen and Verschuren thought that pairs maintained a bond from one breeding season to the next. Rosevear (1969) believes that the West African sun squirrels have two breeding seasons, July to September and November to January. East African records from southern Uganda and western Kenya consist of one pregnant female in November, two in December and one in January; some young in January and March and a lactating female in July. Females not in breeding condition have been collected from Uganda, one in February, one in April, two in July and three in August. Eight females from southern Tanzania were not breeding between February and April.

The time of reproduction may be determined by the males, as they evince signs of a sexual cycle. Not only do their testes fluctuate in size, but they develop two large anal glands, which reach their largest size at the same time as the testes. In Uganda, I collected a male in this condition in mid August and another in February. Further study of their reproductive biology would be very interesting.

The young are born in nesting holes; one to five young per litter have been recorded.

African Giant Squirrel (*Protoxerus stangeri*)

Races

<i>Protoxerus stangeri centricola</i>	Uganda
<i>Protoxerus stangeri bea</i>	West Kenya
<i>Protoxerus stangeri cooperi</i>	Northwest Tanzania and South Uganda



The most striking characteristic of the giant squirrel is its thickly-haired, black and white barred tail. Twelve races have been described and there are two published discussions of their zoogeography and systematics (Verheyen, 1960; Amtmann, 1965).

Three main types of body colouring are discernible: a red one, a yellowish type and a grey-shouldered, yellow-rumped form.



**African Giant
Squirrel**
(*Protoxerus stangeri*)

Family

Sciuridae

Order

Rodentia

Local names

Kisila (Kiragoli), Shiseera (Kitiriki),

Kipare (Kuamba), Kelerebwe

(Luganda)

Measurements
head and body

220—306 mm

tail

260—355 mm

weight

545—734 g

Amtmann's study correlates colouring with climate according to Gloger's rule. Both *P. s. centricola* and *P. s. bea* are russet-bodied forms with somewhat greyish heads; they vary in the intensity of red colour on the rump. There seems to be a greater difference between the populations to the west and south of Lake Victoria and those on the northern shore. The squirrels of Sango Bay Forest appear to be identical to those on Kungwe Mountain, east of Lake Tanganyika; in this race the grey of the head and forelegs is more extensive than in *centricola* or *bea*, while the rump and hindlegs are a grizzled yellow rather than red. Many faunal differences are observable between the forest of Sango Bay and the forests to the north (see Kingdon, 1971 and Vol. I, p. 73), so that the recognition of a racial distinction in *Protoxerus* is interesting. This race was first collected on Kungwe Mountain by Brian Cooper of the Tanganyika Game Department.

The giant squirrel is sparsely haired on parts of the belly, often revealing a yellow tint to the skin. The coat is much coarser than that of any other species of tree squirrel. The claws are large, curved and very sharp and both hands and feet bear very prominent pads. Booth (1960) says they may weigh over 900 g, but I have not found an East African squirrel approaching that weight.

The giant squirrel is exclusively limited to well-developed high forest in tropical areas, depending more upon the height of the trees than on the forest's extent and is also common in swamp forest. It occurs in some mountain areas of the eastern Congo up to about 2,100 m and probably ranges that high also in parts of East Africa.

The nests are not frequently seen because of their high canopy habitat. Sanderson (1940) reports a large spherical nest, very high up in the fork of a branch. The nest measured about a metre in diameter. He was told by the local Cameroonians that such structures were used by the squirrels for several seasons in succession.

Nut kernels and seeds are their favourite food and stomach contents generally consist of a well-chewed white mush. In areas where the oil palm, *Elaeis*, grows, the fruit pulp and the nut kernel of this tree form the most important single item of diet. They also eat the strongly scented fruit of the swamp forest tree, *Pseudospondias*, and the fragrant pulp and seeds of *Tetrapleura*. Other trees such as *Musanga*, *Parinari*, *Chrysophyllum*, *Carapa*, *Caloncoba* *Cordia*, *Urera* and *Phoenix* also provide important foods. Many of these fruits drop to the ground and the squirrels may forage for them on the forest floor, either eating them on the spot, when the pods are heavy, as in *Tetrapleura*, or carrying the fruit away to be stored. Sometimes they can be seen purposefully carrying a fruit or nut in the mouth from one tree to another. Rahm and Christiansen (1963) reported a captive giant squirrel storing food in its sleeping box. This animal ate maize, rice, bananas, paw-paw and pumpkin. Leaves and fibrous matter that appeared to be bark have been found in one stomach and ants in another. In Buganda they are reputed to kill nesting hornbills, Bucerotidae, whilst in captivity they have been reported to take meat.

Where their habitat has been greatly reduced they may go out from gallery forest into grassland to forage. Durrell (1954) writing about the Cameroons describes an early morning foray:





“there were eight of them hopping out into the grassfield. They were large and rather bulky animals, with heavy heads, but the largest and most flamboyant parts of their anatomy were their tails. They hopped cautiously from tussock to tussock pausing to sit up on their hindlegs and sniff carefully in the direction they were travelling. Then they would get down and hop forward a few more feet, flipping their tails as they moved. Sometimes they would crouch perfectly still for a few seconds, their tails laid carefully over their backs, the bushy ends hanging down and almost obscuring their faces. The ones in the grassland were silent, but in the trees behind us we could still hear an occasional suspicious ‘chuck’ from those that had not yet plucked up the courage to descend”.

If disturbed these shy animals freeze, flattened and spreadeagled behind the boughs of large trees. If frightened on the ground or in light vegetation they make for the nearest tall tree. The most commonly heard noise is a loud chuck, which increases in frequency if the animal becomes more alarmed. They are sometimes seen in small groups and a chittering noise can be heard as they play in the trees. When captured they can be very threatening and growl ferociously. Durrell called the noise an “awesome gurking, a cross between a snarl and a snore”. He also described the strange early morning chorus made by the giant squirrel:

"it started like a groan and as it got louder it took on a throbbing vibrating note, the sort of thrumming you hear from telegraph poles—the sound seemed to blur and waver, like a gong hit very softly, rising to a crescendo and then dying away".

They are often to be found in the same tree as a troop of monkeys and are not afraid of them. The crowned hawk-eagle, *Stephanoaetus coronatus*, is probably as much a predator of this squirrel as of monkeys, and I have found a tuft of *Protoxerus* hair near the perch of one of these birds.

Females with foetuses have been collected in December (one), in January (one) and lactating females in December and August. Three small juveniles have been collected in late October. In West Uganda, Robert Glen (personal communication) described seeing two males pursuing the same female in July. I have also watched a male chasing another animal, presumably a female, whilst carrying his tail very erect with all the hairs standing out sideways at ninety degrees to the axis. When light catches the tail in this condition it becomes almost incandescent.

The tail is evidently a very important signalling device for this species and the visual transformations wrought by a change of posture have been discussed in the profile of squirrels.

It would be very interesting to investigate further the behaviour of the giant squirrel, particularly action sequences, sounds and special postures of the body and tail, all the more so because this animal is flamboyant and noisy and these characteristics might be highly evolved.

Ground Squirrels

Xerini

Ground-dwelling squirrels are widespread, being found in many of the drier, colder or more mountainous areas of Eurasia, America and Africa. However, they belong to two distinct tribes: the Xerini and the Marmotini. The latter are distributed over the breadth of Eurasia and down the length of North America.

Outside Africa, the Xerini are represented by a relict species in Persia, and Moore (1959) has stated that it seems certain that the Marmotini have replaced the Xerini as the dominant ground squirrel phylum.





Unstriped Ground Squirrel (*Xerus rutilus*)

Family Sciuridae
Order Rodentia
Local names
 Kindi, Kidiri (Swahili), Ekunyuk,
 Ngikunyuko (Karamojong), Eetata
 (Kiliangulu)

Measurements head and body

200—255 mm

tail

180—225 mm

weight

300—335 g

Unstriped Ground Squirrel (*Xerus rutilus*)

Races

Xerus rutilus dorsalis Western Kenya and Karamoja
Xerus rutilus rufifrons Northern Kenya
Xerus rutilus saturatus South-east Kenya and North-east Tanzania

This small stripeless ground squirrel is heavily ticked with white on a reddish background. The races named above may not reflect any real distinction between neighbouring populations. Although Hollister (1919) warned that staining with local earths might give a misleading idea of colouring, colour is in fact the criterion on which the races were originally described. As with *Xerus erythropus* and many other mammals, lighter colouring is discernible in populations living in drier habitats, darker colouring in those from a more humid environment.





Living in rather more arid country than the striped ground squirrel, *rutilus* is the typical ground squirrel of northeastern Africa. However the two species are sympatric over part of Uganda, Sudan and Kenya, where they meet their respective eastern and western limits.

The two species look superficially much alike but for the smaller size and lack of a side stripe in the present species. Anatomically they are sufficiently different to be considered as distinct genera by some authors.

The striped ground squirrel has an extra upper premolar and much more powerful cheek teeth. The general form of the skulls, particularly the zygomatic arches also differs somewhat. Furthermore, it has been discovered that the ticks parasitizing the two squirrels even in the area of sympatry, are quite different and specific to their hosts.

The feeding habits of this species probably resemble those of the striped ground squirrel but, since it inhabits a zone of unreliable rainfall and less cultivation, the unstriped squirrel is less associated with human activities and its choice of foods must be considerably reduced. Wild roots, pods, seeds, fruit, stems and leaves with some animal food (mostly insects) probably make up the greater part of this species' diet.

Very little is known of their biology. A pregnant female was collected in September, another in November, while small juveniles collected in most months of the year suggest that at least some breeding is going on throughout the year.





**Striped Ground
Squirrel**
(*Xerus erythropus*)

Family
Order
Local names

Sciuridae
Rodentia

Kindi, Kidiri (Swahili), Kamujje
(Runyankole, Luganda, Runyoro),
Ayita (Lwo), Ekunyuk (Itesot),
Locheluk (Karamajong), Viu (Alur),
Majerogo (Lugbara), Afo (Madi)

Measurements
head and body

297—463 mm

tail

184—267 mm

weight

500—945 g

Striped Ground Squirrel (*Xerus erythropus*)

Races

<i>Xerus erythropus lacustris</i>	Uganda
<i>Xerus erythropus leucoumbrinus</i>	Northwestern Kenya
<i>Xerus erythropus microdon</i>	Southwestern Kenya

The colouring of these ground squirrels seems to be correlated with the relative humidity of their habitat and it is possible that the races above might intergrade.

Sandy colouring, a white stripe and ground dwelling habits serve to identify this species in the field. At close quarters, the coarse, bristly hair, long digging claws and very small ears are distinctive features.

This species is distributed from Mauritania across Africa to southwestern Ethiopia and Kenya. It is primarily an animal of the open woodlands and Sudanic savannas, but it ranges through most of the belts that lie between the arid edges of the Sahara and the tropical rain forest. In Uganda, I have seen these squirrels colonizing newly cleared forest land before the farmer had grown his first crop.

They dig their own burrows where this is necessary or possible, but in most areas the chambers of termitaria need little modification to provide the squirrels with a shelter. In rocky areas they may live in crevices and holes. There are generally several entrances to a central chamber, which is lined with dry grass and small twigs. Where several squirrels have concentrated over a period of time, separate units may join up and a small complex of burrows and chambers may develop; however each individual generally sleeps alone in its own chamber. The passages are seldom more than one and a half metres long and generally much less than a metre deep.

Their presence is a very characteristic feature of cultivated land in Uganda, as they live on the edge of "shambas", where they sometimes steal newly planted seed and also groundnuts, cassava, yams, sweet potatoes, bean pods, young cotton bolls and maize cobs. Watson (1950) reports them digging away the bases of maize plants until the stem falls. Their natural foods are roots (Watson notes a favourite as *Hydnora hanningtoni*), grass seeds, storage leaf bases of some grass species, green leaves, fallen fruit, nuts and *Acacia* pods. They do not often climb and are clumsy at it, but may clamber into fruiting shrubs to get at the fruit. They eat eggs, young birds and small reptiles and are said to steal the eggs and chicks of poultry. They eat a variety of insects. One animal I picked up one morning run over on the road, had a third of its stomach filled with winged termites which had been flying the night before. These had presumably been gathered in the early morning before the birds had dispatched them.

They are a familiar sight to most travellers of the murrum roads of Uganda. This is probably a reflection of their fondness for the conditions that accompany the ribbon development of road-side settlement and cultivation. They are bold and inquisitive, frequently rising on their heels to get a



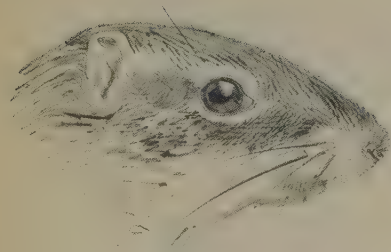
Seeds of *Canarium* opened by *Xerus erythropus*.



Left forefoot, *Xerus erythropus*.



Right hindfoot, *Xerus erythropus*.



clearer view over the grasses, and sight must play an important part in their lives. They seem particularly sensitive to, and aware of, flying birds, which is probably indicative of where their greater dangers lie, from hawks and eagles. Snakes, particularly the puff adder, *Bitis arietans*, are also important predators together with servals, other wild cats and also jackals.

They walk in an unhurried manner, with frequent pauses for sniffing or peering about, but they can run very fast in a continuous series of long leaps. The tail is carried behind when walking or running but, very frequently, it is raised when the animal stops or rests. Little flicks of the tail are common when the squirrel is relaxed but it bristles like a bottle brush when the animal is excited or angry.

Their vocal communications have been described as having four tones with a variety of modulations. Their chatter of excitement is similar to that of some other squirrels.

They appear to defecate haphazardly outside the burrow, the dung being formed into dry and slightly elongated pellets.

Sanderson (1940) reports them as aestivating in an erratic way and they are thought to be able to live on their fat like marmots in time of drought. They carry nuts to their burrows, where they can open them in safety. Their skill and neatness in opening the very hard shells of *Canarium schwiensfurthi* are striking (see drawing). The study of these animals has been neglected, their social structure and behaviour, for instance, seem to have never been properly investigated. The effective range of an individual from his home burrow and the uses of the burrow are also not known. This neglect is unfortunate for the animal is a nuisance to farmers and foresters. It has been especially castigated for digging up the seeds of *Gmelina arborea* in Uganda Forest Department nurseries.

Furthermore, as a familiar of human activity it may be a potential vector of disease. *Xerus inauris* has been found to carry rabies in South Africa and also harbours trypanosomes. More important, several deaths or near deaths have been reported as caused by the bite of these animals. Watson (1950) records a child being bitten in Teso and dying within an hour of returning home. Again, a Makerere student was bitten in 1962 by an utterly fearless animal entering a university hall, and the man only survived a prolonged fever because of painstaking medical care. It would seem that the bite may readily transfer pathogenic organisms of danger to man.

Ground squirrels are often kept as pets by enthusiastic naturalists. They have been known to live up to six years in captivity. Local people hunt them and eat them in some areas.

Their breeding and biology have not been studied. A female that had just given birth was collected in southern Uganda in mid-April and a small juvenile at the end of February. Enquiries suggest that young animals are most frequently seen in the wild between August and October, but some breeding probably continues throughout the year. This species has three pairs of ventral mammae, without a pectoral pair.

Two to six young are born at a time, four being the most usual number. Cansdale had captive young ground squirrels that appeared to be seeking milk by sucking the ears of another genus of squirrel, this behaviour was noticed up to the age of nine weeks (Rosevear, 1969).



Anomaluroids

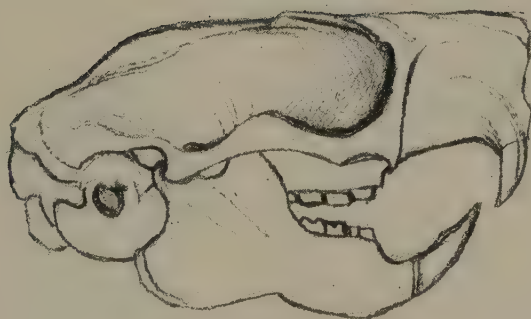
Anomaluroidea

Africa is the home of some very peculiar and little known rodents which have been united by Simpson (1945) in the super-family Anomaluroidea. The majority of named forms in this superfamily are fossils, which were an important part of the African fauna long before modern rodents appeared on the scene. These primitive animals seem to have some resemblances with each of the three rodent suborders. Taxonomists have, therefore, had great difficulty in placing the rodents of this group. Schlosser (1885) connected the anomalurids with the histricomorphs, Tullberg (1899) with the myomorphs and Alston (1876) with the sciurormorphs.

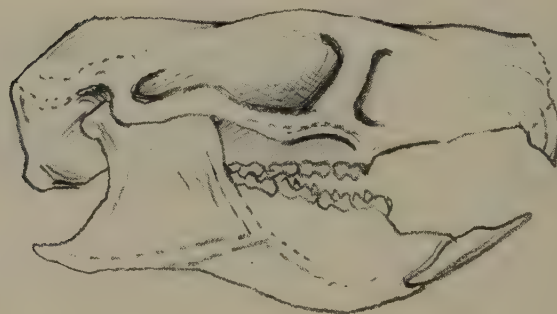
As so often happens with primitive groups, their contemporary representatives only survive by becoming very highly specialized or by hanging on in isolated lands or in very stable refuges. The two living families, the Pedetidae and the Anomaluridae, contain one and seven species respectively. By contrast the extinct families, Pseudosciuridae and Theridomyidae, have been assigned some twenty fossil genera between them.

The anomalures and the spring hare, *Pedetes*, are both highly specialized animals and are fairly widespread, but the anomalurids include a "flightless" form, *Zenkerella*, which appears to be a relic species only found in the Cameroon-Gaboon Refuge, while the tiny *Idiurus zenkeri* is scarcely better off, restricted as it is to a similarly small area of western Africa and also to the Central Refuge.

It is interesting to compare skulls of the Eocene *Pseudosciurus* with the contemporary *Anomalurus*.



Anomalurus derbianus.

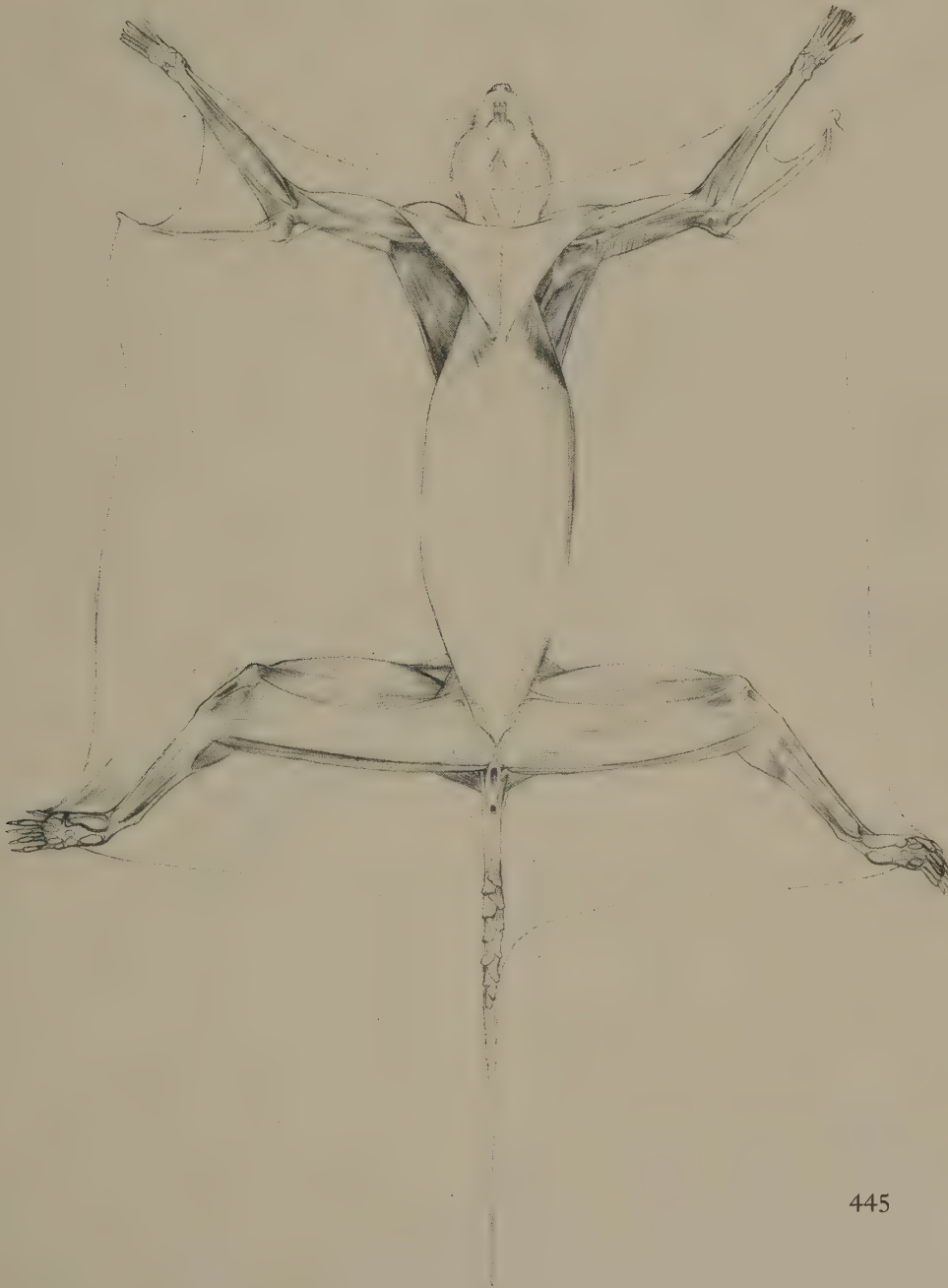


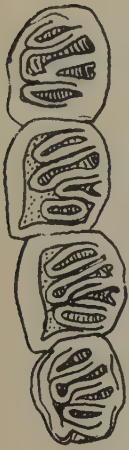
Pseudosciurus (Eocene anomaluroid).

Anomalures, "Flying Squirrels", Scaly-tails

Anomaluridae

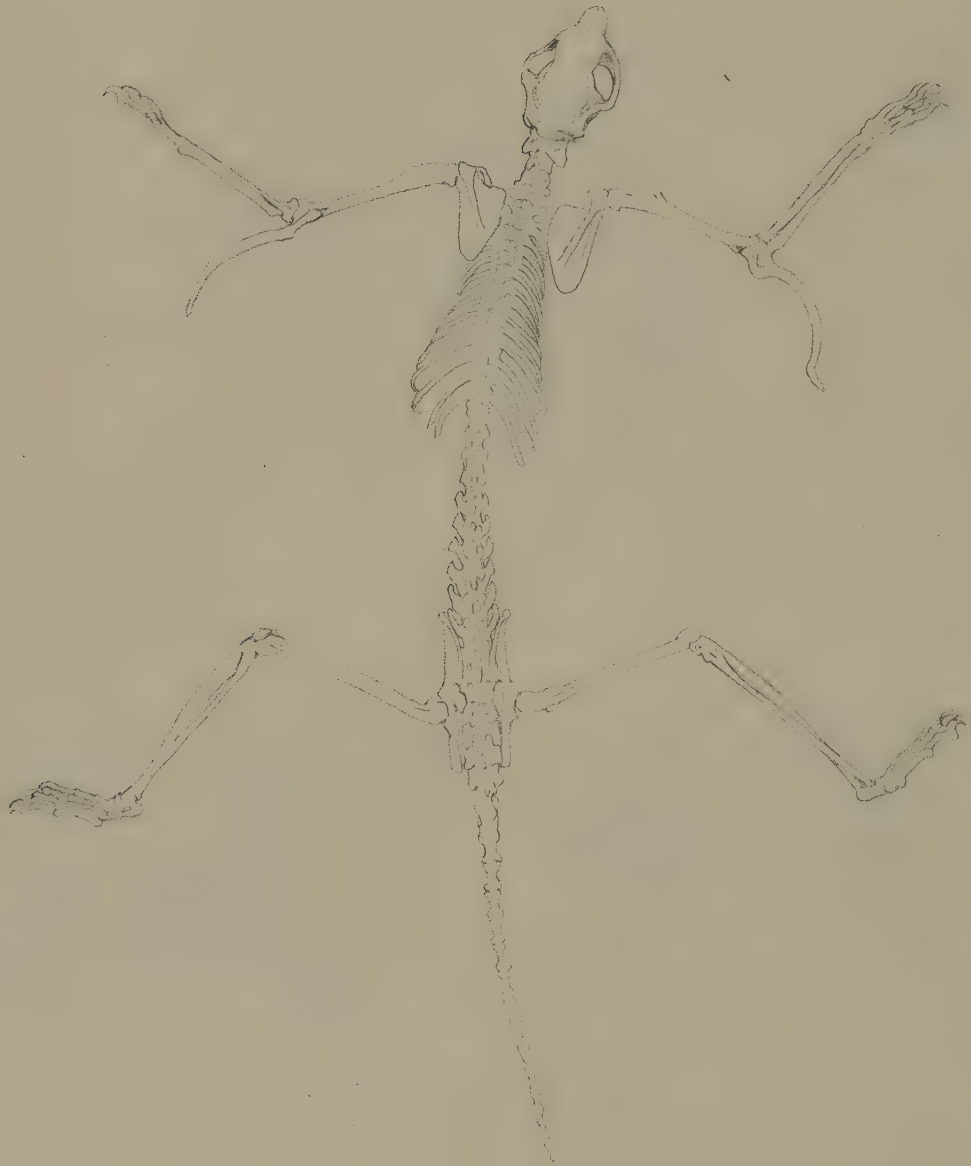
The anomalures are a group of uniquely African rodents that occupy the niche of "gliders" on this continent. The same niche is filled by the true squirrels in Eurasia and America, and by the flying phalangers in Australasia. Quite different devices have been evolved in each of these groups in order to extend the body's surface and turn it into a controllable volplane.



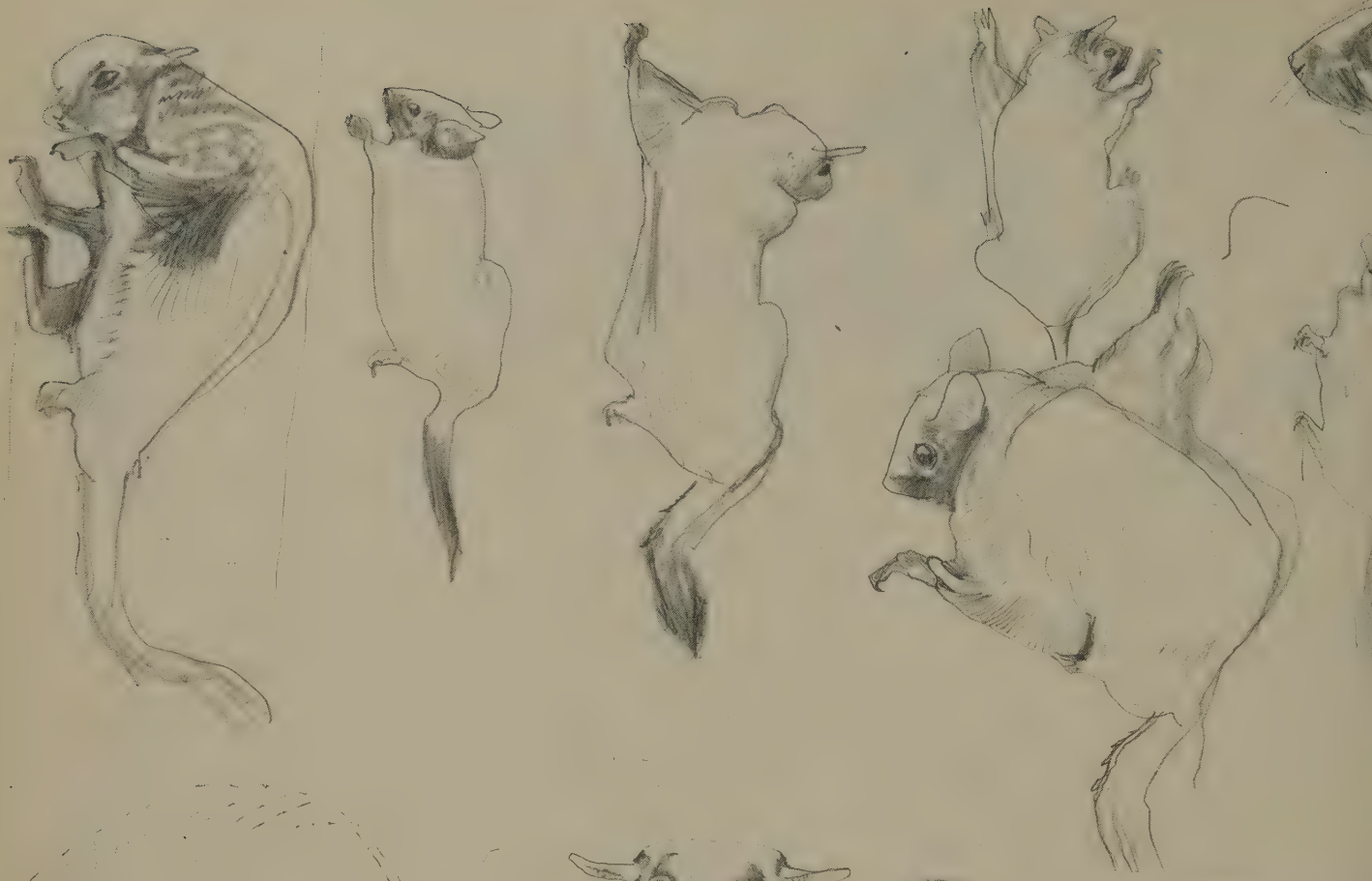


There is an interesting West African form called *Zenkerella*, which is flightless. Unless this represents a degenerate condition it might resemble the early stock of rodents from which its gliding relatives evolved. The scaly underside to the tail is well developed and it would be interesting to know more about this animal's detailed anatomy, gait and habits.

In all the other forms of anomalures the gliding membrane extends between the tail and the hindlegs, and from the hindlegs forward to a special cartilaginous strut which grows from the elbow; a smaller membrane extends from the neck to the wrists. The membrane consists principally of skin, but



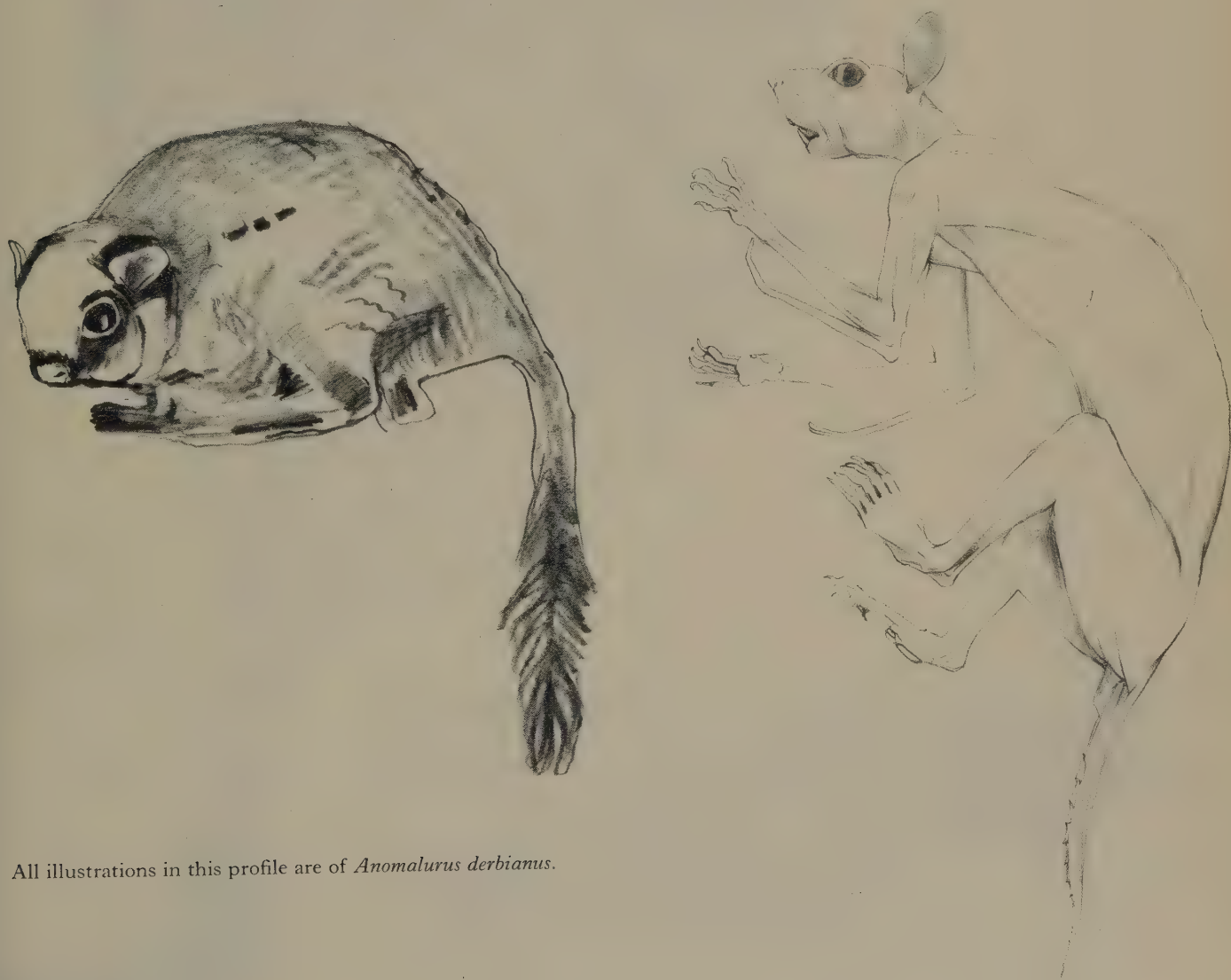




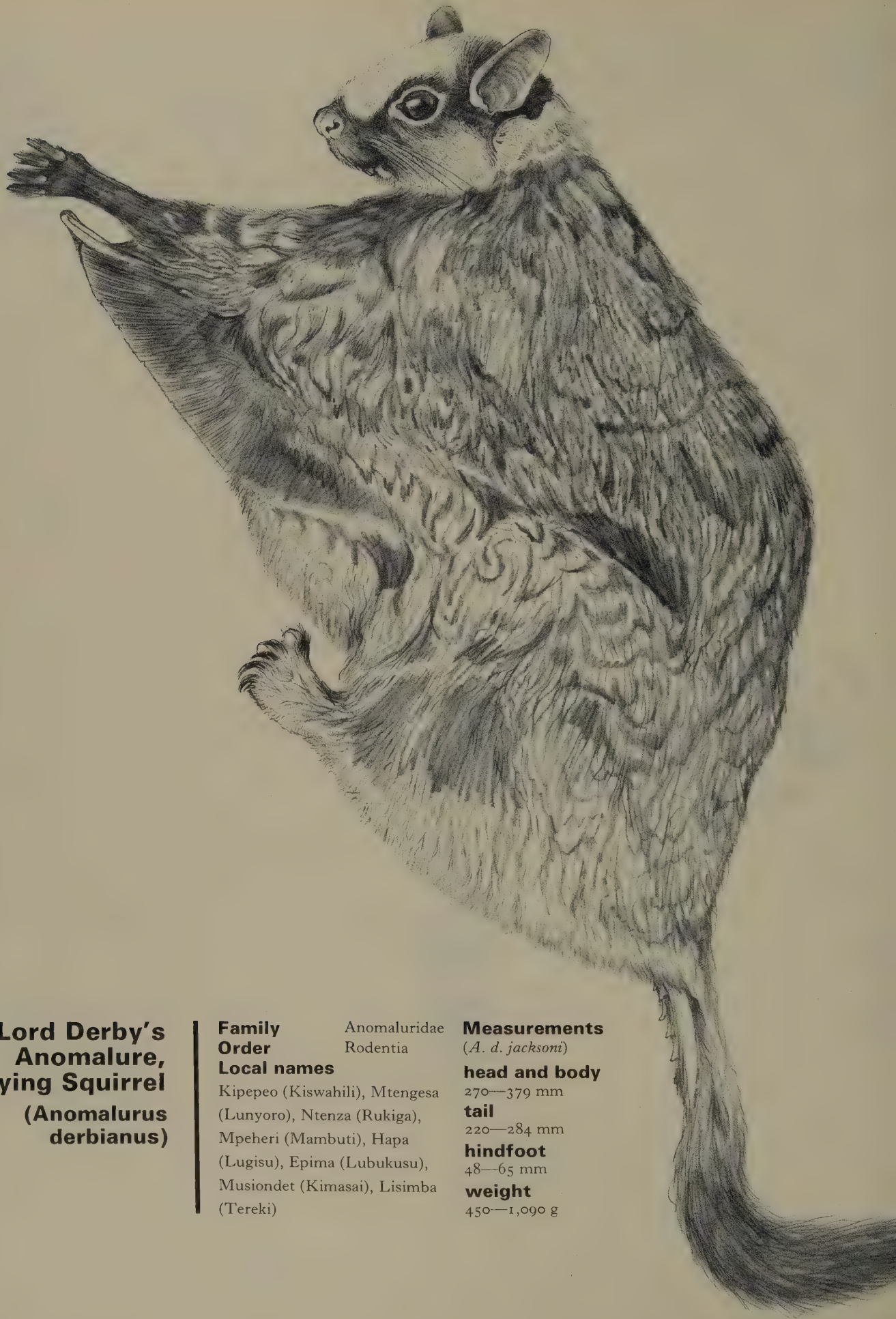
longitudinal muscle fibres run through its length. These are inserted at the front edge behind the biceps and line the inner surface of the triceps. It is the contraction of this muscle which folds up the membrane when the animal is not in flight.

The body and the limbs of *Anomalurus* are very slender and long. The skeleton is so lightly built that, although strong, the bone of some processes is transparently thin. Its fur is lighter and finer than that of chinchilla or persian cat and is very long on the back with a grizzle to the tips. It is reported to give off static electricity and sparks on occasion. By contrast, the hair growing on the outer-forward edge of the membrane is stiff and bristly, serving to increase the rigidity of the membrane behind the elbow strut.

When one compares the largest East African form *Anomalurus derbianus jacksoni* with the tiny *Idiurus* it is apparent that there is an interesting correlation between the weight of the animal and the total area encompassed when the membrane is spread. The former has an area of about 900 sq. cm to 900 g, the latter about 50 sq. cm to 15 g.



All illustrations in this profile are of *Anomalurus derbianus*.



**Lord Derby's
Anomalure,
Flying Squirrel
(*Anomalurus
derbianus*)**

Family Anomaluridae
Order Rodentia
Local names
Kipepeo (Kiswahili), Mtengesa
(Lunyoro), Ntenza (Rukiga),
Mpeheri (Mambuti), Hapa
(Lugisu), Epima (Lubukusu),
Musiondet (Kimasai), Lisimba
(Tereki)

Measurements
(*A. d. jacksoni*)

head and body

270—379 mm

tail

220—284 mm

hindfoot

48—65 mm

weight

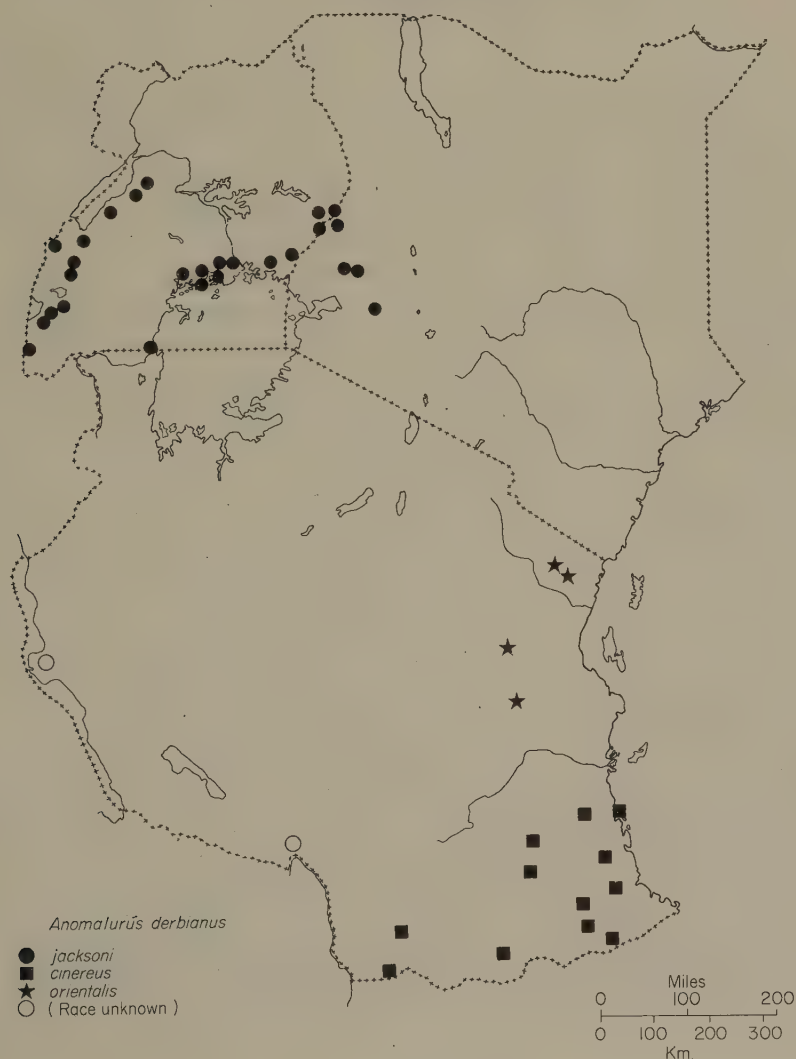
450—1,090 g

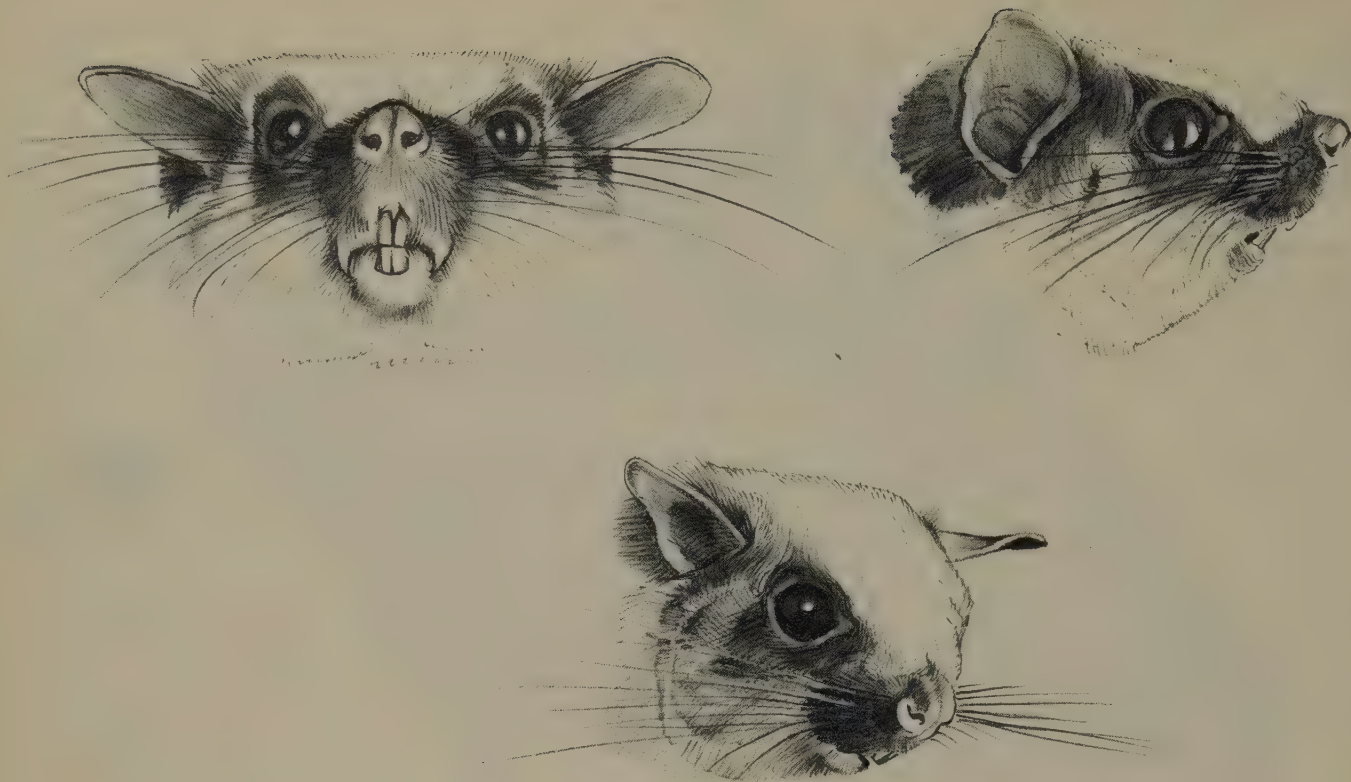
Lord Derby's Anomalure, Flying Squirrel (*Anomalurus derbianus*)

Races

<i>Anomalurus derbianus jacksoni</i>	Uganda and western Kenya
<i>Anomalurus derbianus cinereus</i>	Southern Tanzania
<i>Anomalurus derbianus orientalis</i>	Usambara and Uluguru Mountains and Southern Highlands

This anomalure is a surprisingly large and heavy animal, considering its gliding, aerial way of life. The largest form is *A. d. jacksoni* which is dark grey with a silvery grizzle to the tips of the very long, exquisitely fine-textured fur. Silver is most extensive round the head and shoulders, becoming an almost uniform pale grey on the forehead. Black fur masks the eyes and surrounds the ears and black bristle hairs reinforce the hem of the membrane behind the cartilaginous elbow strut. In the Mt Elgon population there is a chocolate brown suffusion on the fur of the membranes and legs.





The southern *A. d. cinereus* is a smaller animal and of a paler grizzled grey with yellowish tints. The montane *A. d. orientalis* is a dark cinnamon colour also with a strongly marked grizzle. Other races occur in the Congo and West Africa. The species' total range extends from Sierra Leone to western Kenya and from Angola and Zambia to southern Tanzania.

Lord Derby's anomalure is extraordinarily adaptable and successful, having by far the widest range of any of the Anomaluridae and occupying an unusually broad spectrum of vegetation types for such a specialized animal. It is, perhaps, most numerous in lowland forest but it is not uncommon in some montane areas, being found up to 2,400 m on Mt Elgon. The southern populations live in *Brachystegia* woodland or riverine forest.

Wherever these flying squirrels live they are very dependent on natural shelters because they do not make nests. The favourite site is the interior of a hollow tree trunk and dead trees are particularly favoured. This probably accounts for the frequency with which they are found in or near villages and cultivation, for many of the bigger tree trunks are left standing after the canopy and the undergrowth have been destroyed to allow cultivation (sunlight for the crops is often let in by simply ring-barking the larger trees). These conditions suit the anomalure and also bring the animal to people's attention more easily. In the "miombo" woodlands *A. d. cinereus* has developed the habit of sheltering in the hollowed-out tree trunks which serve as bee-hives. Many honey gatherers from the southern region of Tanzania complain of these unwelcome tenants, which enter the hive by gnawing a round hole starting at the crack where the lid rests on the lower half. The prevalence of this habit does, of course, make the animal more familiar, but it is also possible that bee-hives have allowed it to extend its range more widely in the "miombo" woodlands, for suitable hollow trees are probably less com-

mon than empty bee-hives. The species of tree used for shelter is unimportant, except that some types are more prone to have rotten or hollow centres or deep fissures and cavities.

This anomalure is principally a bark and fruit-eater, but flowers, leaves, green nuts and insects have also been recorded. A favourite food is the bark of *Strombosia scheffleri*; the presence of this tree in any quantity is usually an indication that Lord Derby's anomalure will also be about. The tree has a smooth, flaky bark, rather like that of the plane trees of the northern hemisphere. Small branches and twigs are gnawed in an irregular way by flying squirrels, but the branch is hardly ever ring-barked and only the cambium is eaten so that no permanent damage is done to the tree. A characteristic notch is sometimes made into twigs and Rahm (1969) found small gnawed branches at the base of the home tree. He listed some of the following tree species as providing edible bark: *Cynometra*, *Staudtia*, *Klaenedoxa*, *Pentacletha*, *Lebrunnea*, *Carapa*, *Neoboutonia* and *Syzygium*. *Cynometra* is related to *Brachystegia*, and since Lord Derby's anomalure occurs in areas where each of these trees is a dominant species, their barks and leaves might be presumed to provide a staple in such areas. The green fruit of *Syzygium* and *Carapa* are eaten as well as *Myrianthus* and *Cynometra* leaves. I have seen an anomalure feeding on the orange flowers of *Loranthus*. Cansdale (in Rosevear, 1969), Sanderson (1940) and others have also noticed flowers being eaten and a captive from Mt Elgon ate rose petals and hibiscus flowers. Meal worms are eaten in captivity. I kept a captive for six months on fruits, mainly bananas with a vitamin supplement, sweet potato tops and guava tree bark. Rahm fed his captive on a similar diet plus "gateau pour singe", a fortified rice mixture.

The bulk of their food is eaten *in situ* although some items may be carried back to the shelter. The animal reaches its arm or arms out and grasps flowers or fruit firmly in the hooked hand, it then draws it to the mouth rather as a monkey would. Nuts, twigs and fruit are held in both hands and gnawed.

Rahm (1969) found the cubic capacity of the stomach to be about 50 to 60 cubic centimetres. With the viscera removed, the weight may be reduced by about half; considering how slender the muscles of anomalures are and how lightly built their skeletons, this is perhaps not surprising.

Anomalures do not put the whole weight of their body onto the scaly tail while climbing as has sometimes been asserted. The scales play only an incidental role in climbing which is achieved by the limbs; in any event the muscles and bones of the tail are not constructed to be heavily stressed. According to my observation, the function of the scaly tail is related to the normal passive resting posture in which the animal often spends all its daylight, and some of its nocturnal, hours. The claws on all four limbs resemble those of "hanging" bats and the Indonesian flying lemur, *Cynocephalus*, in having very sharp, thin, hooked blades. These hooks are well suited to suspension, but unlike the bats and the flying lemur, anomalures do not hang freely but lie against a surface, their weight slung between the limbs. Some point of abrasive contact in the nether region is unavoidable; the scales, therefore, serve a primarily protective function and provide some passive support for the resting body.

The glide of the Lord Derby's anomalure is an impressive sight. If the animal has been frightened out of its hole by hammering the trunk, it may





come out with such rapidity that its first movements are invisible; if unafraid, it may sit at the entrance of its hole and survey its surroundings before kicking itself off into space. The big muscles of the thigh undoubtedly provide the main propulsive force for this launch. The animal does not stretch its limbs out at once, but gains momentum for its flight by dropping a metre or more, travelling some four or five metres from the trunk before beginning its glide which can be astonishingly level. At any point in a directional glide the animal can change direction, even making a right-angled turn or bank. The landing is made with a quadrupedal stall, the forearms and legs coming down and forward to form an air-trapping bag. The distance of a glide depends very much on the site. One glide observed by me covered about a hundred metres, but my Mutwa guide said he had seen an anomalure leave the same hole and glide the entire length of the open valley, a distance of about two hundred and fifty metres. This site at the end of a valley was well placed for a long flight. In most habitats the anomalure is probably opportunistic, finding shelters between four to twelve metres from the ground wherever these can be found.

These animals very rarely come to the ground, but “flying squirrels” have been known, from time to time, to land at night on the floors of lighted verandahs or even in rooms (Rosevear, 1969). When forced to move on the ground they hop in a rather rabbit-like fashion. The synchronized push of the hindlegs also provides the main motive force when climbing a tree and the body arches in a series of very rapid leaps up the vertical surface. By contrast the animal scurries rather like a squirrel when travelling head down on a vertical trunk. On thin branches the most agile acrobatics are displayed; often the fore-parts of the body will flip through the space made between the hindlegs as the body hangs suspended by the hooked hindclaws. These animals are mainly nocturnal and they return a pale cool eyeshine in the light of a torch.

Like some other nocturnal species they enjoy sun-bathing and have sometimes been seen clinging to a tree on one spot on which sunlight was falling. My captive regularly came out to sun-bathe between about 8.30 and 9 in the morning. In the evening, they become active shortly before dusk and, in cool conditions, even earlier; for instance, I have seen one out at 4.30 p.m. on an overcast day. Rahm (1969) timed one as it left its tree on at least ten occasions, and found that it almost always left within a few minutes of 6.30 p.m. His captive, on the other hand, was about earlier, coming out for an hour between five and six and then returning to its box until 8 p.m. when it emerged for the night.

Anomalures have acute sight and hearing. I have noticed the head being moved from side to side as an animal looks intently at its surroundings. The ears too “revolve” sensitively. Like the head movement the ear movement also seems to be in a horizontal plane. Rahm thinks that the acoustic surveillance of the surroundings may be more important than the visual one. The role of smell is difficult to assess. The animal itself gives off at times a very strong odour reminiscent of that of some monkeys. The females sometimes exhibit two small subcutaneous glands in the lower abdomen, but it is not known whether scent plays any part in their sexual or social life. When it is shot, the eyes often give out a copious secretion that looks like milk.

The vocal repertoire of this anomalure appears to be limited. Quiet bouts

of low purring have been heard and a twittering noise is also reported; they hiss menacingly when caught.

The optimum density for these animals probably depends on a variety of unknown factors: their feeding requirements, seasonal food fluctuations and their special need for adequate shelter. They seem to be attached to their home tree in the forest and Rahm found a tree that was thought to have been used by one animal for at least two and a half years. On the other hand, Ionides (personal communication) stated that *A. d. cinereus* in southern Tanzania made local movements which were determined by the fruiting of their favourite trees.

Pairs have been noticed sharing a tree and mothers with young are usually found in the same hole. Larger associations are also known; the manager of a sawmill described to me occasions when six or eight animals have taken flight from a single tree during felling operations. A tantalizing glimpse of their behaviour in the eastern Congo was reported by Riddell (1948), who had made himself a platform about eight metres up a tree. This was one of about seven large trees in an "arena". Late at night under a bright moon, six anomalures appeared scuttling about the trunks and repeatedly landing right beside Riddell, suggesting that their gliding paths were well established. The animals repeatedly did a round of the seven trees, humping up a trunk into the canopy, running out to the end of a branch, pausing and then planing down in a long swooping glide to end in a slight upward stall on another tree five to eight metres up, and then up to the top of that tree and off again to the next. Some seventy flights, varying in length between seventeen and eighty metres, were made in the space of about an hour. After this period of intense activity the animals disappeared until dawn, when they appeared once again for a brief period of play. Rosevear (1969) too reports a Nigerian resident watching a "family" of anomalures emerging regularly at sundown.

These animals can be caught easily if a net is put over their exit holes. In the eastern Congo they are also caught in nooses laid over the hole. One tribe, the Watembo, use the rather aromatic stomach content of anomalures as a relish on their food. The pigmoid Batwa used to demand this animal as part of the dowry paid to the prospective father-in-law. Presumably its capture was a mark of the future groom's competence in woodcraft.

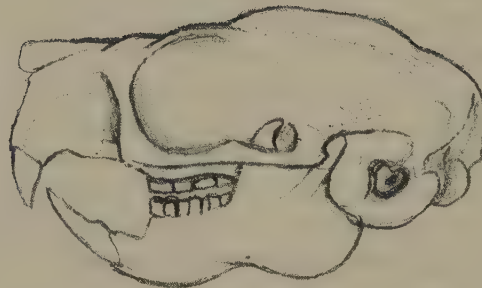
Very little is known of the breeding behaviour and biology of anomalures. For Uganda and western Kenya I have the following records: four births in January, two pregnancies in March (one large and one small embryo), lactating mother in May, a fairly small juvenile in July and a slightly larger one at the end of October. Males with well-developed testes have been collected in February, July and December. Females not in breeding condition have been collected at the same time as breeding ones, implying that a clear-cut season is unlikely in the equatorial zone. The West African *Anomalurus peli* has two litters a year. Ionides found most females of *A. d. cinereus* with well grown young in May and June (early dry season), while the males were alone at this time so that seasonal breeding is more likely to occur in these southern woodlands. The gestation period is not known. A vaginal plug has been reported to form in the female.

The young are probably born in the hollow tree or other form of home shelter. They are large, well-furred, with open eyes and active at birth, with



a head and body length of about 160 mm. The female has two large pectoral nipples and produces copious milk. The milk glands are placed behind the armpit and along the edge of the pectoral muscle. One young per litter is usual but two or three have been recorded. Sanderson (1940) says that the young perch in the shelter and are fed by both parents until nearly fully grown. The parent fills its cheeks out "to the size of a tangerine" with well masticated food which it brings to the young. "Fully grown" may be an exaggeration, however, since quite small animals have been collected that were apparently fending for themselves. As old animals may measure as much as 350—370 mm from the nose to the root of the tail and may weigh a kilogram, it is interesting to record that a male weighing 625 g and with a head and body length of 295 mm already had well-developed and active testes.

A species of malarial plasmodium has been found in Lord Derby's anomalure. I noticed numerous small worms in the peritoneal cavity of some Uganda specimens from lowland forest. Loveridge (1937) noted that some montane *A. d. orientalis* were quite free of internal parasites.



Lesser Anomalure

(*Anomalurus pusillus*)

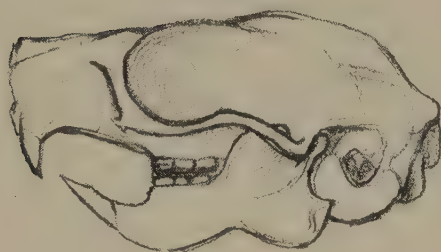
This anomalure is very like *A. derbianus* on a smaller scale. It can be distinguished from the young of the latter by a yellow tinge on the belly and the absence of black round the ear.

This species has a less extensive range than *A. derbianus*, being confined to the main African forest block, from the Cameroons to western Uganda. Its relative scarcity is affirmed by Rahm (1969), who, after many years collecting in the eastern Congo (Zaire), listed data for only three specimens.

The lesser anomalure is stated to occur in Ankole by Hopkins, who thought it likely to be widely distributed in the western part of Uganda. I have not yet seen it.

They probably have similar habits to *A. derbianus* and Rahm (1969) recorded one feeding exclusively on *Musanga* fruit.

This species roosts in tree holes, cracks and hollow trunks.



Lesser Anomalure

(*Anomalurus pusillus*)

Family Anomaluridae
Order Rodentia

Measurements

head and body

210—246 mm

tail

138—157 mm

hindfoot

37—47 mm

Beecroft's Anomalure (*Anomalurus beecrofti*)

This species has highly distinctive colouring, being light grizzled grey above with a white spot between the ears, underneath it is yellowish with a rich orange throat and midline on the belly. The tail is much less bushy than that of Lord Derby's anomalure.

The species is included in the fauna of East Africa on the strength of a voluntary and detailed description of this animal by a reliable Mambuti informant who has seen these anomalures in Bwamba Forest (see Vol. I, p. 45) and who was responsible for the collection of the first specimens of *Idiurus* recorded for East Africa.

According to this informant their presence in Bwamba is linked with the oil palm, *Elaeis*, an association that was pointed out by Dekeyser and Villiers (1951), who found this species feeding on nothing else. Other authors have also listed various fruits and leaves. Beecroft's anomalure is found from Sierra Leone to the Semliki, a similar distribution pattern to that of *Elaeis*.

This species has been described as diurnal, and individuals have been observed roosting on the outside of trunks of trees and palms, relying on their cryptic coloured fur for protection. They do not seem to use holes to roost in.

This animal is much less common than *A. derbianus*, even in West Africa, and fewer specimens have been collected. It appears to be anatomically more specialized, with a very narrow palate and muzzle. The tube of the nasals and premaxilla is exceptionally well developed extending the nose well forward of the incisors.

Nothing is known of their social or reproductive biology. A species of microfilaria has been discovered in the blood of the West African *A. b. hervoi* (Dekeyser and Villiers, 1951).

Beecroft's Anomalure (*Anomalurus beecrofti*)

Measurements head and body

253—310 mm

tail

186—238 mm

hindfoot

37—55 mm

weight

650 g





**Dwarf Anomalure,
Flying Mouse,
Pygmy Scaly-tail
(*Idiurus zenkeri*)**

**Family
Order**

Animaluridae
Rodentia

**Measurements
head and body**

68—79 mm

tail

91—117 mm

hindfoot

15—17 mm

weight

14—17.5 g

Dwarf Anomalure, Flying Mouse, Pygmy Scaly-tail (*Idiurus zenkeri*)

At a quick glance this tiny animal resembles a very silky-furred, tawny-coloured mouse; however, it carries on its sides membranes like those of the larger anomalures and there is a scaly area beneath the tail. The tail itself is lined on the underside by two rows of short stiff hairs and has sparse, soft long hairs on the upperside (20 mm).

The niche occupied by this little animal must be very exacting for there is an extraordinary convergence of form between *Idiurus* and the South Australian feather-tail glider, *Acrobates pygmaeus*. This marsupial has a very similar "feathered" tail, and almost identical measurements; it lives in groups numbering over a dozen, shelters in hollow branches and seems to have similar habits to *Idiurus zenkeri*.

There are two species of *Idiurus*, of which *zenkeri* is the smaller. The larger species, *macrotis*, is often found sharing the same roosts and might also turn up in Bwamba Forest.

Idiurus zenkeri is found in the Cameroons and in the Central Forest Refuge. This restricted range suggests that it is a specialized and ancient form linked to the most stable areas of lowland forest and that it is not capable of colonizing new habitats created by forest expansions. It is unknown in montane areas.

Small colonies of these animals have been found sheltering in the hollows and large cracks of various types of trees, but larger colonies seem to favour huge hollow trees that are virtually empty shells. Some types of trees are more likely to provide these conditions than others and Rahm (1966) has listed colonies of *Idiurus* he found living inside *Klainedoxa*, *Pseudoprosopis*, *Paramacrolobium*, *Gilbertiodendron*, and *Pentaclethra* species.

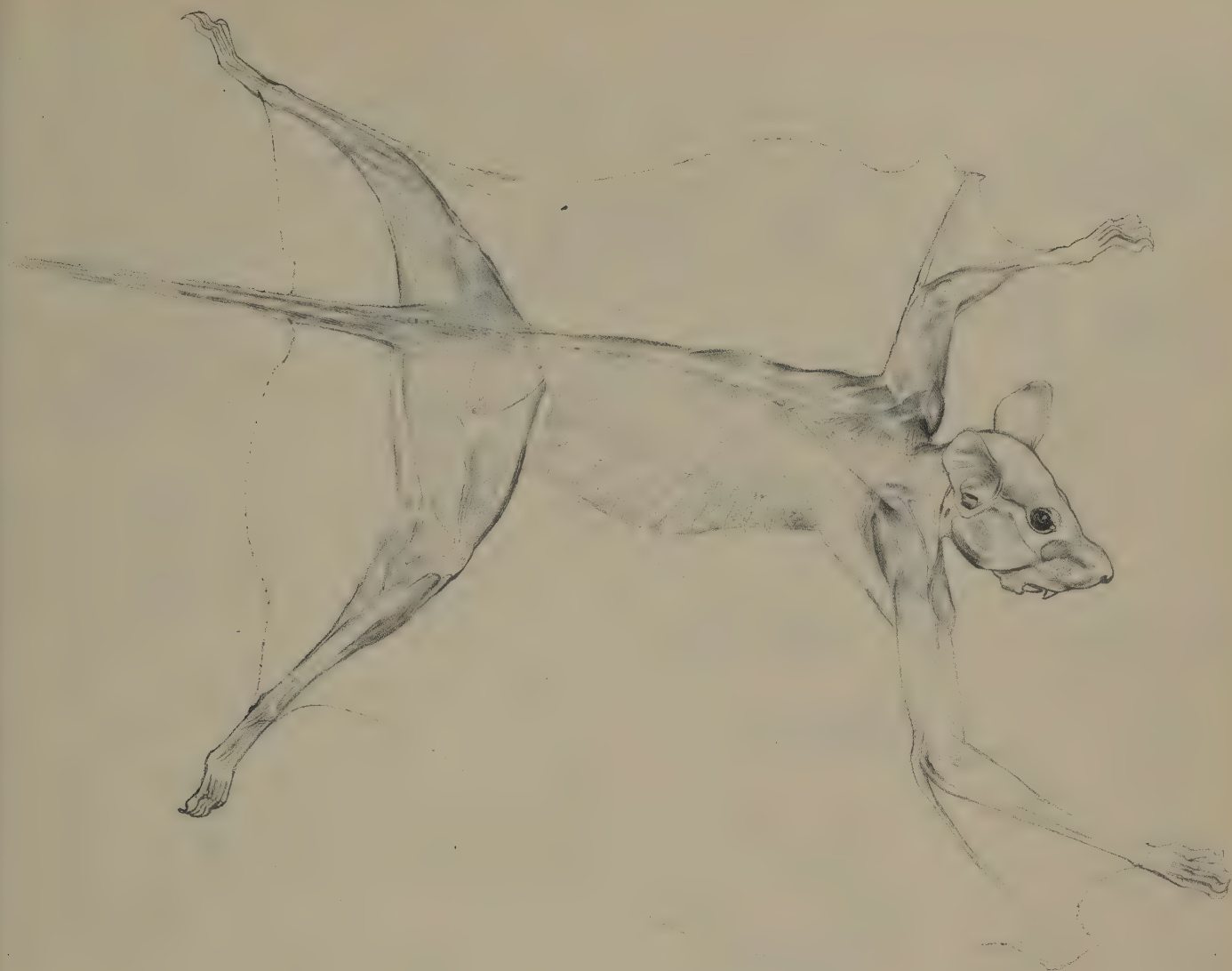
Durrel (1954) described an *Idiurus* tree shelter in the Cameroons that is very similar to one in Bwamba Forest, in which I observed a colony of these animals.

"We approached the trunk of the tree and I saw that there was a great arched rent in the wood, between two of the flanges; this hole was about the same size and shape as a small church door. . . . I peered upwards (inside the trunk) but a slight bend in the trunk prevented me seeing very far. . . . I laboriously climbed up the inside of the trunk until I was high enough to crane round the corner. The trunk stretched up as hollow as a factory chimney and just as big. At the very summit of the tree there was a large exit hole and through it a shaft of sunlight poured. Then suddenly I nearly released my rather precarious hold with excitement, for I saw that the top part of the trunk was literally a moving carpet of *Idiurus*. They slid about on the rotten wood as swiftly as shadows and when they were still they disappeared completely from sight, so perfectly did they match the background".

In Bwamba, the animals were able to come and go only through the low-level rent which stretched up to about 4 metres from the ground, as there was no high level exit.

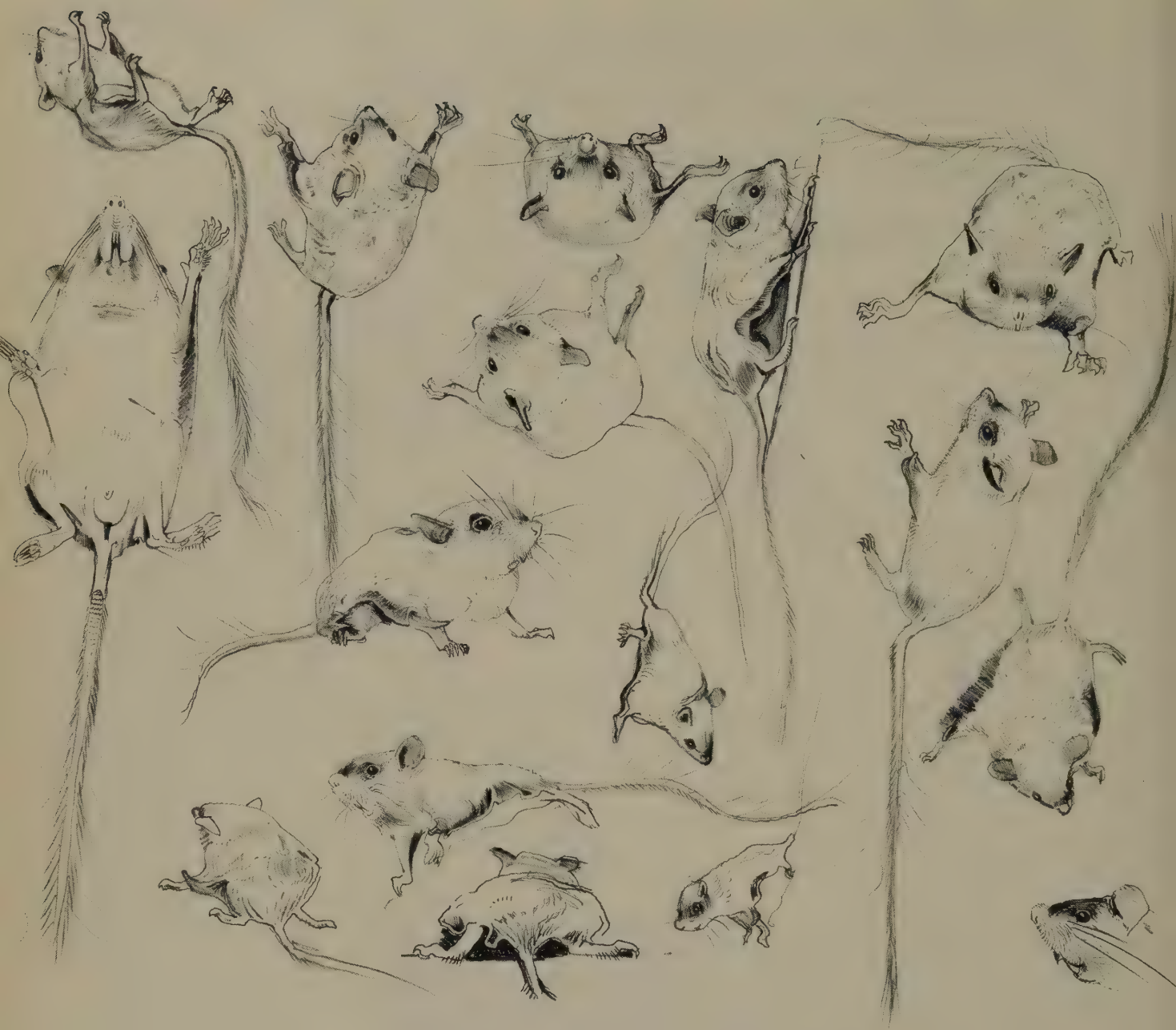
Idiurus are very difficult to keep in captivity, partly because so little is known about their feeding habits. They are known to eat the orange pulp of the oil palm fruit. Durrell had them feeding on avocado pear. Wild specimens





have been collected containing finely ground whitish vegetable pulp which might have been fruit or nuts, also traces of insects and a dark brown liquid, possibly nectar. The captive I kept for a few days seemed to explore bits of proffered food in the manner of other small rodents, turning the object over with the forepaws and occasionally lifting it to the mouth for a nibble. They may be particularly sensitive to temperature, noise or humidity. My captive died on a protracted car journey during which the normal levels of these factors had been disturbed.

The sight of *Idiurus* seems to be good, and, during daylight hours, they run about, glide and generally react to disturbance without signs of distress, although they will seek shelter as soon as they are able. The relatively large ears twitch and swivel in response to noise but they do not appear to be quite as mobile as those of *Anomalurus derbianus*. The very long whiskers obviously play an important role in the tactile exploration of their surroundings. The quadrupedal gait of these animals is quite different from that of the large anomalures, being a scurry in which each leg moves independently rather than in fore and aft unison.



Their gliding has been described by Durrell, who smoked out a large colony:

"They left the trunk of the tree without any apparent effort at jumping; one minute they were clinging spread-eagled to the bark, the next they were in the air. Their tiny legs were stretched out, and the membranes along their sides were taut. They swooped and drifted through the tumbling clouds of smoke with all the assurance and skill of hawking swallows, twisting and banking with incredible skill and apparently little or no movement in the body. This was pure gliding and what they achieved was astonishing. I saw one leave the trunk of a

tree at a height of about thirty feet. He glided across the dell in a straight and steady swoop and landed on a tree about a hundred and fifty feet away, losing little, if any, height in the process. Others left the trunk of the smoke enveloped tree and glided round it in a series of diminishing spirals to land on a portion of the trunk lower down. Some patrolled the tree in a series of S-shaped patterns, doubling back on their tracks with great smoothness and efficiency. Their wonderful ability in the air amazed me, for there was no breeze in the forest to set up air currents I should have thought essential for such intricate manoeuvring”.

Rahm (1966) has illustrated a landing of *Idiurus* with outlines taken from a film sequence showing that the tail comes down and the hindlegs come forward as if to hug the oncoming branch. This evidently creates maximum air resistance at the last moment and ensures a gentle landing.

I caught one dwarf anomalure by hand after it had landed on the ground in an attempt to evade a draped mist-net. It was quite agile but was obviously more vulnerable on the ground than on the smooth, firm bark of a tree, where their turn of speed will take them up a trunk and out of sight in a matter of seconds. Without smoking them out first, I found them reluctant to glide in daylight; they seemed to prefer escaping up the trunk. One attempted to hide under a piece of bark.

The only sound it uttered was a mouse-like squeaking at the time of capture and later in its box, which may be a simple sign of excitement or alarm.

Colonies vary very widely in size, from small groups of a dozen or less to over a hundred. Some of the larger associations involve both *Idiurus* species. Both sexes and all age groups can be found together and, during the day, they sleep in tightly packed groups. Durrell has suggested that they may travel quite some distance:

“The stomach, to my complete surprise, was crammed with the partially digested red husk of the palm nut. This was the last thing I expected to find, for the palm nut is, in the Cameroons at any rate, a cultivated product and does not grow wild in the forest. If the rest of the colony had been eating palm nuts on the night before they were captured by us, it meant that they must have travelled some four miles”.

They share their hollow tree with other species of *Anomalurus*, with the dormouse *Graphiurus*, and also with bats, *Hipposideros cyclops*, *Tadarida leonis* and *Scotophilus nigrata*.

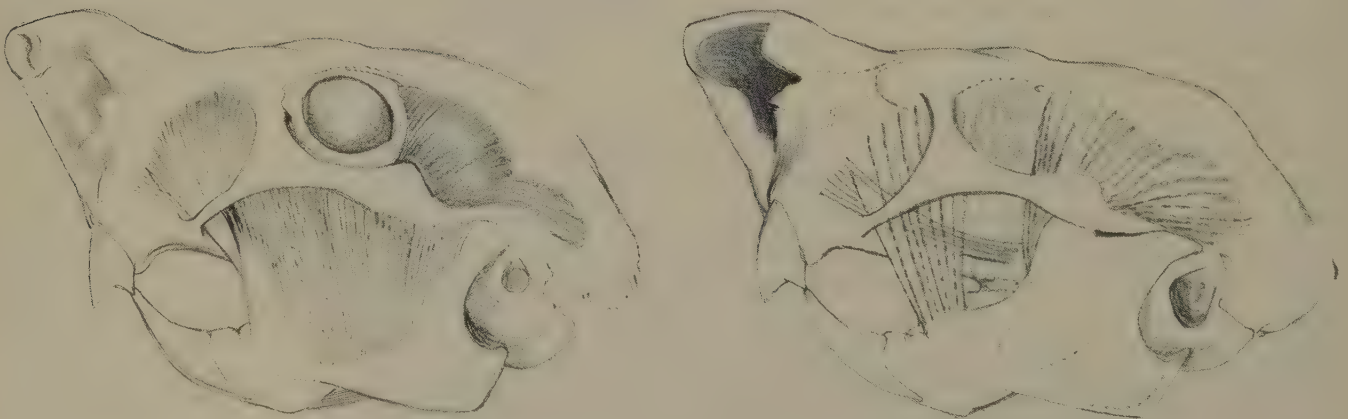
There is little data on the breeding of *Idiurus zenkeri* and what there is is mostly negative. Of four females collected in Bwamba in December, none was pregnant but one exhibited enlarged ovaries; a female collected at the beginning of November was also not pregnant. Rahm records a single juvenile—head and body length 63 mm—caught in July in the eastern Congo (Zaire). He caught 11 females in August and September and three in June but does not record any pregnancies. Males collected in Bwamba in November—December did not appear to have their testes fully developed.

It is possible that females bear their young away from the colonies. It is odd that no pregnancies have been recorded for this species (Rahm found 4 pregnant *Idiurus macrotis* in August and one in June), particularly when one considers the representative number of months covered by Rahm's collection. One young is thought to be usual for this species.

MONTH	MALE	FEMALE	PLACE
January	2	—	Niamiringi
May	3	1	Tshoko
June	6	3	Irangi
July	—	1 juv.	Shabunda
August	—	1	Mashere
August	7	5	Mitala
August	1	2	Biripange
September	1	2	Keba
November	1	1	Bwamba
December	9	3	Bwamba

Idiurus zenkeri might turn up in Kayonza Forest, but to date the species has only been collected in an area of Bwamba Forest that is now being destroyed, and it is possible that this interesting animal might—together with other species—disappear from East Africa altogether once the forest has been felled. As I suggested earlier, *Idiurus* has a very limited distribution and it may have survived to the present day only because millions of years of relatively stable climate maintained a suitable environment for this species. Extremely localized and short-term needs for timber and farm land may, therefore, deprive East Africa of plant and animal species that have managed to survive only in the hot-house conditions of the Central Refuge of which Bwamba is a small part. Modern timber management keeps forest in a seral stage. If this eventually becomes extended to all areas of forest it will ultimately deprive species such as *Idiurus* of their shelters and will cause their extinction.

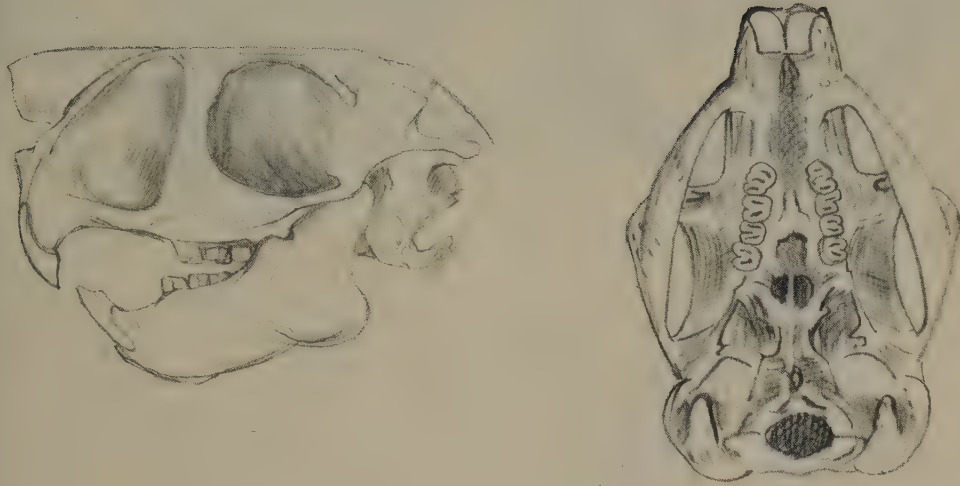
In Volume I there is a discussion on the bio-geographic importance of the Forest Refuges (p. 65) and of Bwamba Forest (p. 45).



Idiurus zenkeri, deep dissection of part of the masseter and the temporal muscle.

Spring Hares

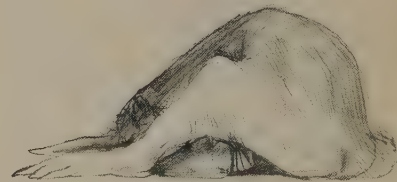
Pedetidae



Taxonomists have been puzzled by the affinities of the spring hare, some placing it with the hystricomorphs, some with the sciurormorphs. Two known Miocene fossils do not help the understanding of the spring hare's origins, for one, *Megapedetes*, is virtually a larger version of the living form and *Parapedetes* is even more highly specialized than *Pedetes*. The majority of taxonomists, however, have recognized an affinity with the anomalurids and Simpson (1945) has placed the Pedetidae within the super-family Anomaluroidea.

Apart from some similarities in the arrangement of the maxillary process and infraorbital foramen, there is little resemblance between the skulls of *Pedetes* and those of the contemporary anomalurids. The architecture of the spring hare's cranium has been completely remodelled by the inflation of the ear bullae, which have displaced all the bones at the back of the head. This enlargement of the tympanic bullae is found in many desert rodents and has been the subject of much speculation. Zavattari (1938) suggested that they amplify vibrations transmitted through the ground and so act as resonators assisting in the perception of vibrations. Cetaceans also have enlarged bullae which are thought to facilitate perception of water-borne vibrations. Heim de Balsac has suggested that desert animals might face the danger of dehydration of the fluid in the middle ear and that the bullae, which are said to contain air with a high humidity content, might avert this danger. The normal resting posture of *Pedetes* brings the flat top of the head into direct contact with the ground between the hindlegs. This posture must allow the animal to pick up the slightest vibrations coming through the earth. The benefits of such increased awareness in an open environment must be numerous and would concern intra-specific relations as well as the detection of predators.

Another peculiarity the spring hare shares with many other desert





rodents, such as the jerboas, *Dipodidae*, the Australian hopping mice, *Notomys*, and the kangaroo rats, *Heteromyidae*, is the huge development of the hindlegs and the adoption of a bipedal hopping gait, which Hatt (1932) has called "ricochetal" locomotion. Considerable force is required to lift a three kilo animal in an explosive leap of several metres. The stout levers of the spring hare's hindlegs are served by very large muscles on the femur and upper tibia, the *rectus femoris* (or *quadriceps*), the *biceps femoris* and the *semitendinosus*. During each hop the body is held horizontal for most of the time; this cantilevering of the body throws the centre of gravity forward and puts a heavy load on the spinal extensor muscles. These muscles also maintain the posture of the head and body when not jumping and are extremely large. Hatt believes that the great bulk of the *latissimus dorsi* is responsible for a unique conformation of the sacral spines; these have had to rise above the muscle in order to provide a skeletal anchorage for the lumbo-dorsal fascia, on which there are important muscle attachments.

In Volume I (p. 86) the spring hare was described as a single balanced cantilever: the body is balanced on a fulcrum which lies between the hip joints, and the main architecture of the skeleton is centred on the pelvis. In the sitting postures, the centre of gravity is shifted behind the hip joint, either by raising the head and shoulders towards the vertical, or by flexing the back strongly so that the heavy lumbar region is carried directly above the fulcrum. The centre of support is the point where the toes rest on the ground, but a slight "tripod" action may come into play when some weight is taken by the tail. The tail, however, is most important as a counter-poise because of the



single transverse plane of balance in a bipedal animal, a function for which its relatively heavy musculature and big hairy brush are well suited. Such a finely balanced cantilever has environmental limitations, as it is ill-adapted to manoeuvre broken and irregular ground, or country bearing anything more than the lightest vegetation.

Another skeletal feature that betrays this limitation is the needle-like form of the vertebral spines. Quadrupeds tend to have broader spines and one functional reason for this flattening is thought to be to guard against lateral strains. Observation suggests that the spring hare's way of life in its chosen habitat does not demand great capacity for manoeuvring among obstacles. According to Hatt, the marked backward slope of the thoracic spines behind the neck is influenced by increased bending of the neck, which is a means of meeting the changed and more effective angle at which the *spinalis dorsi* muscles exert their pull. The increased height and strength of the lumbar vertebrae and their forward inclination are due to the heavy load put on them by the very large dorsal extensor muscles and the *quadratus lumborum*. The weight of the animal is taken on the four well-nailed toes, particularly on the very stout third toe and the two shorter ones flanking it.

There are also many less obvious peculiarities concerning the anatomy of



spring hares. Coe (1969b) remarks:

“The most striking feature of the male and female reproductive organs is the great length of the tracts, particularly the penis and vagina, but whether or not these modifications, together with the forward positioning of the kidneys and ovaries close to the diaphragm, result from the highly specialized hindlegs and lengthening of a very mobile pelvis, which swings to and fro through an angle of 45° with the long axis of the vertebral column, remains conjectural”.

The four cheek teeth of *Pedetes* are peculiar in lacking roots and growing continuously. The tooth patterns are reversed in the lower jaw, the lobes being united on the lingual side in the upper teeth and on the buccal side in the lower jaw. Their structure has been discussed at length by Wood (1965).



**Spring Hare,
Pedetes**
(*Pedetes capensis*)

Family
Order

Pedetidae
Rodentia

Local names

Kamendegere (Kiswahili), Kesi
(Kigogo), Jibu (Kinyaturu)

Measurements
head and body

350—450 mm (ave. 400)

tail

370—480 mm

weight

3—4 kg (ave. $3\frac{1}{2}$)

Spring Hare, *Pedetes* (*Pedetes capensis*)

This very peculiar animal cannot be confused with any other. Almost exclusively nocturnal, it reveals itself by the bright red reflection of the eyes, which pick up light from a great distance. When seen in the field the animal appears to have only two legs, so diminutive and so completely hidden are the forelegs when folded on the chest. The spring hare is sandy yellow brown in colouring with a white underside and a black brush to the tail.

Pedetes are distributed mainly throughout the semi-arid steppes of eastern Africa and southwestern Africa, with scattered populations occurring in the intervening country, although they are apparently absent from northern Zambia.



Wherever they occur, spring hares are limited to sandy, relatively open flats. They dig their own burrows and the soil in which they dig their holes



must be sufficiently firm not to collapse without, however, being hard, stony or clayey. Situations which offer these ideal soil conditions may be found around the shallow lakes of the eastern Rift Valley, in wide alluvial valleys and flat sandy plateaus where vegetation has been reduced or degraded by overgrazing.

The animals' preference for open, flat country is probably influenced by their gait. When jumping at speed, the bipedal leap or "ricochet" is very unstable and is unsuited to circumvent obstacles or to traverse broken land. Their very sharp-clawed but small forelimbs are used both to expose food and to dig their burrows. Large mounds of sand are excavated around the entrances of many of these holes, but some are dug in such a way that no sand mounds form. Roberts (1951) suggests that they usually emerge from these "clean" holes; he was told by a sportsman that

"he often secured spring hares by waiting at the exit of one of these holes at dusk and, just at the fall of darkness, when they would spring out and be silhouetted against the sky above the level of the thorn trees for a moment, he would shoot them".

If the animals are as sensitive to vibrations as is generally supposed, it is likely that they were aware of the hunter's presence before they emerged, for they do not usually leap out of their burrows in such a dramatic fashion.

The burrows are simple passages, generally less than a metre deep, sometimes, however, they plunge deeper into the ground and may twist and turn in an apparently haphazard way. Spring hares dig rapidly and often seal their holes with sand after entering them.

Their foods are mostly dug from near the surface or "grazed". They eat stems and roots, the storage bases of grasses, the new sprouts of many types of plant, low foliage and herbs and the fruits of many shrubs and climbers, including various Cucurbitaceae. Where agriculture has invaded their habitat they may take to crop raiding, eating sweet potatoes, groundnuts, pumpkins, maize and growing wheat. Locusts and beetles have also been reported as items of diet. They return night after night to a favourite feeding area in order to dig up grass and eat the roots. Shortridge describes these patches as resembling hoed ground. The tops of some grasses are completely rejected.

Spring hares are very alert, with keen hearing, scent and sight. Their enormous eyes are adapted to night vision and strong sunlight or torch-light seems to dazzle them; indeed, they can often be approached very closely when dazzled by a powerful light. This may be due to the very poor performance of the iris sphincter. They have occasionally been seen about in daylight.

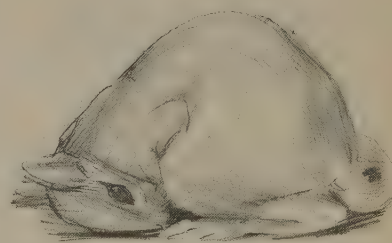
When searching for food they proceed somewhat like a hare, taking the weight on the short forelimbs for each lobe of the hind legs. As soon as they are alarmed, however, they rise onto their hindlegs and advance by bipedal hops; usually these hops cover one or two metres, but, when great momentum has been achieved, bounds of six or eight metres are possible and even greater distances have been claimed for their leaps.

Spring hares are generally quiet animals. When wounded they are often silent, but may make a bleating noise sometimes; a chorus of grunts is a sign of excitement among a group of spring hares. Their activity probably varies with the seasons. The time of emergence from the burrow is influenced by the weather and possibly by the phases of the moon. They seem to dislike rain and do not come out in wet weather. The burrow is generally plugged when the animal goes to earth in the early morning and when attempts are made to dig the animal out a series of plugs is encountered.

Very little is known about the social life of spring hares. Captive groups live amicably together and prefer to sleep in a crowd. Wild groups of eight or nine animals can be seen in close proximity to one another at night. However, when their burrows are dug out, single animals or at most a pair with one young are found together, although there may be other animals in neighbouring burrows. In favoured localities, such as are found in parts of the Rift Valley, in Kenya and in the Singida district in Tanzania, concentrations of 30 to 40 animals may inhabit a relatively small area. For instance, I have watched a large concentration of spring hares living on a broad sandy flat which was circumscribed by rocky outcrops and a belt of thick *Commiphora* bush on one side and the shore of a shallow lake on the other.

They tend to be rather localized and probably do not roam far from their burrows. However, during periods of severe drought there have been reports of spring hares travelling 10 to 40 km in a night in search of food and water. Ansell (1960a) says that there is circumstantial evidence of fluctuating numbers.

Various carnivores feed on *Pedetes* and I have found a striped weasel,



Poecilogale, run over on a track that passed by a colony of spring hares. Serval cats, *Felis serval*, caracals, *Felis caracal*, wild cats, *Felis libyca*, genets, *Genetta*, ratels, *Mellivora* and black backed jackals, *Canis mesomelas* are all common carnivores sharing the spring hares' habitat. They have been reported killed by the mongoose *Herpestes*. Alan Root (personal communication) has twice seen a genet sitting outside the entrance to a spring hare's hole, apparently in ambush. The bat-eared fox, *Otocyon*, is another carnivore with a similar range and habitat to that of the spring hare, but because it feeds mainly on insects this little fox is no threat to a large rodent; however it may enlarge and use spring hares' burrows for shelter, since it is not adept at digging.

Pedetes is a unique and interesting animal. Its anatomy, gait, reproduction and behaviour are in important respects unusual and different from other rodents. Relatively easy to keep and also tame with little inclination to bite, it is a promising animal for zoos and laboratories, although it has a slow reproductive rate. Its vulnerability and nuisance value in the face of current agricultural expansion will jeopardize its long-term prospects outside the national parks.

The breeding of the spring hare has excited some interest, for, like the anomalures, it generally bears only one very large young in an advanced stage of development. The young is well-haired and active at birth and the eyes open on the second day. When there are two young, which is rare, these may be identical twins. Van der Horst (1935) pointed out the unusual circumstance of an animal that is well sheltered in a burrow bearing but one young and apparently gaining no reproductive benefit by the security of its burrow. Probably the young stays in the burrow for a long time; Coe never succeeded in collecting an animal under 1,473 g in weight.

Like the anomalures, spring hare females have 2 pectoral mammae. Females—presumably in oestrus—have been seen soliciting the male's attention by raising the rump and tail in a "presenting" gesture and by wagging their hindquarters in his face. The gestation period is not known but is probably in the region of two months. Coe (1969b) believes that in East Africa the young are born throughout the year, but it is possible that peaks occur, for Hollister noted seven out of nine females pregnant in early August. In Zambia, a birth season is thought to occur between November and February (Smithers, 1966). The one young is born in an unlined chamber and is nearly a third of the size of an adult; it weighs between 240—280 g. Births have been described in detail by Hediger (1950b) and by Coe (1967a).

Captives have been kept for nearly eight years. In an attempt to assess the age of spring hares one student embarked upon the extraordinary academic exercise of extracting bacula and eye lenses, using the weight of these organs as criteria of relative age (Smith, 1965).

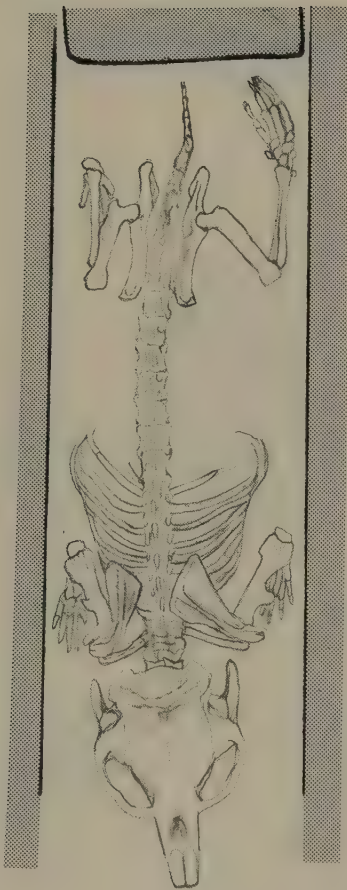


Mole-rats, Blesmols, Root-rats

Bathyergidae, Rhizomyidae

In all parts of the world rodents have discovered the subterranean niche and at least five completely independent lines of rodents have adapted to a mole-like existence. None have specialized more than the exclusively African Bathyergidae, but all have converged to a remarkable degree.

Very interesting comparisons can be made in East Africa, because mole-rats belonging to two independent stocks are present: the Bathyergidae and the rhizomyid *Tachyoryctes*. One of these interesting comparisons concerns their anatomy and suggests a correlation between form and function. The two animals have quite different pelvic girdles and, since blesmols push earth with their backsides while root-rats push with their chest and faces, many of the stresses and strains on this structure probably operate in opposite directions. (See drawings below.)



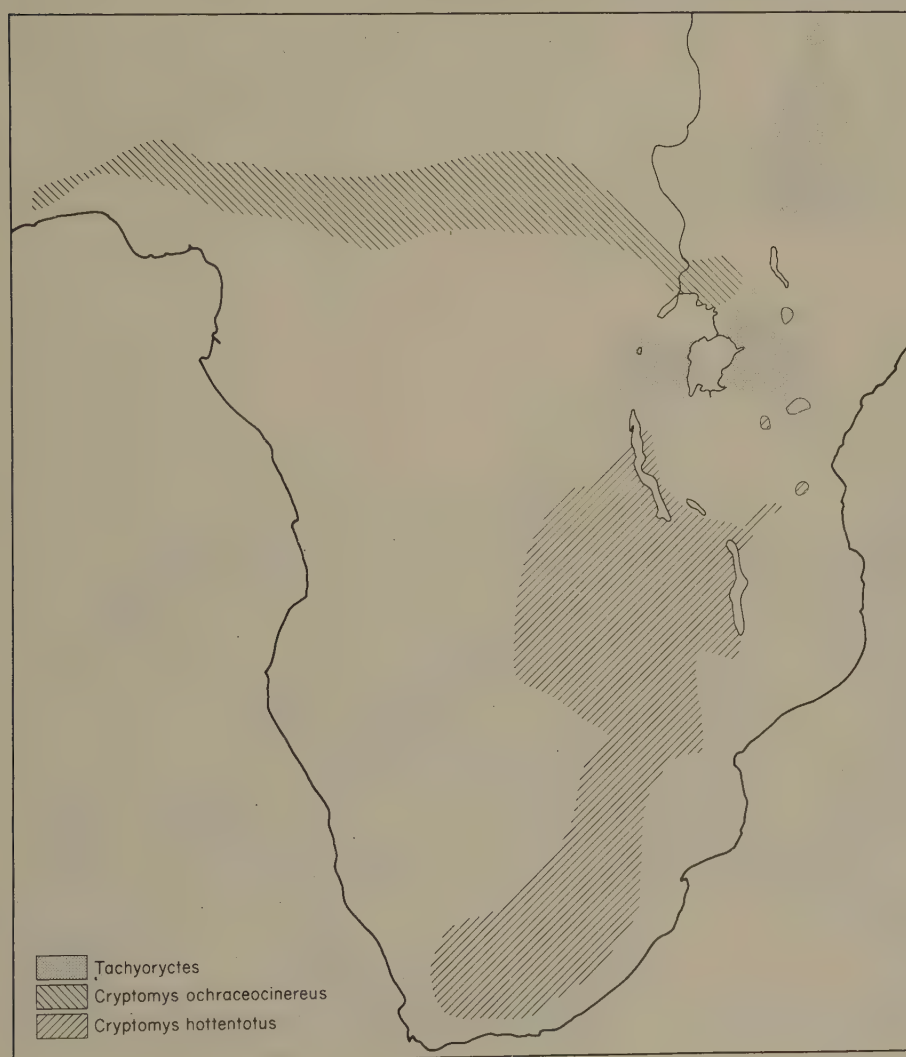
Cryptomys pushes earth with its hindquarters.



Tachyoryctes pushes earth with its head and chest.

Another interesting problem suggests itself in a comparison of the distribution of *Tachyoryctes* with that of the blesmols, each of which seem to occupy a distinct ecological niche. *Tachyoryctes* co-exists with *Heterocephalus* at Moyale and with *Heliophobius* on the Loita Plains, at Kiambu and in some other localities that are perhaps marginal for both species. However, there appears to be no overlap between *Tachyoryctes* and *Cryptomys*, although they occur in close proximity near Kigoma, which is the extreme southern limit for *Tachyoryctes* and the northern limit for *Cryptomys hottentotus*. The western *Cryptomys ochraceocinereus* meets its limits with the Victoria Nile and its extensions, the lakes Kyoga and Salisbury. To the immediate south and east of the Victoria Nile, *Tachyoryctes* is the only subterranean mole-rat and, since much of this strip must have carried forest in the recent past, there is a strong implication that *Tachyoryctes* is both a dominant species and a more effective colonizer than the blesmols. In this way *Tachyoryctes* is neatly interposed between two populations of *Cryptomys* that are probably isolates of what was once a single population.

It is evident that *Tachyoryctes* has not evolved as far as the blesmols and



this may make it a more adaptable animal. In fact, it competes only for the most favourable habitats and with the least specialized form of blesmol, *Cryptomys*. The limitation of the root-rat to the northeastern quarter of Africa and the presence of relatives in Eurasia suggests that its ancestral stock may have invaded Africa long after the African blesmols had occupied a variety of distinct niches.

Various factors could contribute to the dominance of *Tachyoryctes*, not the least being its aggressiveness. There is little doubt, however, that *Tachyoryctes* is ecologically superior, for it is able to survive at far greater densities on smaller plots of land. Its food is ubiquitous, its diet catholic and it expends a minimum of energy in burrowing.

Verheyen and Verschuren (1966) found that a small colony of *Cryptomys* had dug an extensive burrow system over 300 m long. By contrast a single *Tachyoryctes* can live in a burrow of less than 20 m in length and within a very dense population—one animal occupying only 140 sq. m space. (See Rahm, 1971.)

There may be many more facets to this situation, which offers fascinating possibilities for a detailed comparative study.



Blesmols

Bathyergidae

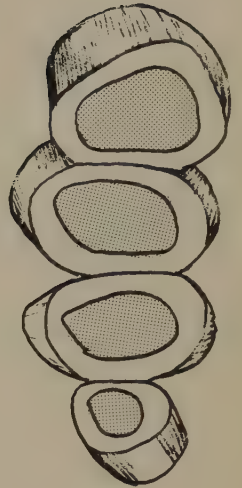
The blesmols are an exclusively African group. Two Oligocene fossils from Eurasia, *Cyclomytus* and *Tsaganomys*, once thought to be Bathyergidae, are now classified in the Ischyromyidae (Piveteau, 1958).

The relationship of blesmols to other rodents is problematic, because the skull, which is the structure used to trace affinities, has become extremely specialized. Simpson (1945) says

"There are few more doubtful points in classification concerning animals that are fairly abundant and quite well known than the affinities of the bathyergoids . . . everyone agrees that they are extraordinarily isolated among rodents and . . . a definitive arrangement cannot be expected until less specialized ancestral forms are found".

The most obvious specialization of the skull is the subservience of the entire structure to the incisors and the muscles that operate them. Indeed, at a first glance, the head seems to consist of little else but a brain box welded onto the incisors, with broad bony ridges and flanges for muscle attachments (see drawing p. 362).

Blesmols are similar to other subterranean digging animals in that they have cylindrical, short-limbed bodies, strong, blunt heads, no external ears and blind eyes. The fur is adapted to be rubbed both ways and the testes are carried inside the body cavity. They have a great sensitivity to vibrations.



This is betrayed by the structure of the middle ear and modifications of the cerebellum (Hill *et al.*, 1957). The degenerate eyes have acquired a secondary function, the surface of the very thick cornea having become very sensitive to air currents.

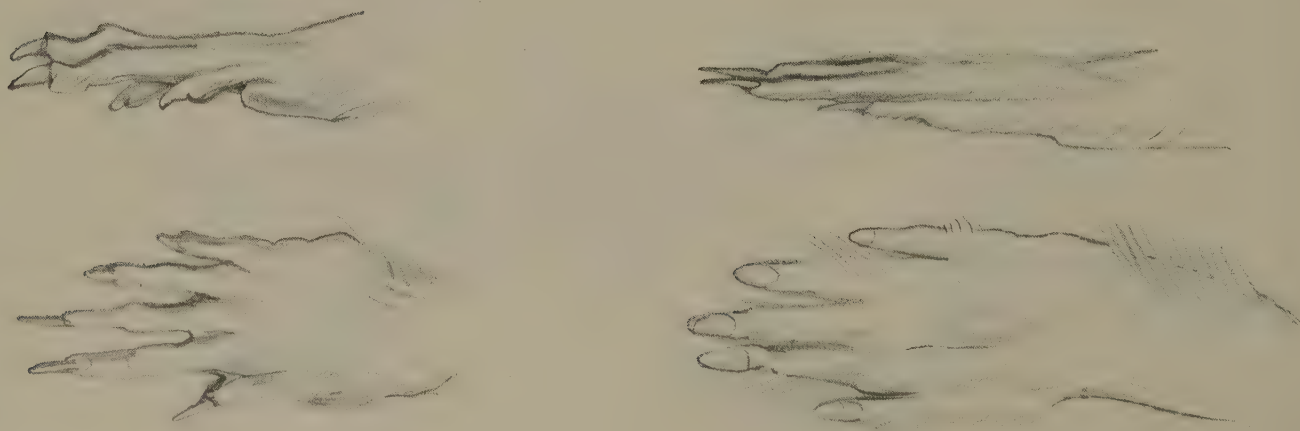
"Genetically, the cornea of *Cryptomys bigalkei* offers a good example of positive adaptability. The eyes of *Cryptomys* when open, indeed serve a useful purpose for the detection of the position of air currents from burrow perforations, but when the mole-rat is digging with its lower incisors it will be clear that dust and sand grains would get on the cornea. . . . Mutations for thicker corneal epithelium would naturally be beneficial and of survival value". (Eloff, 1958.)

The same author (1951a) observed a habit that could be correlated with this sensitivity. He saw the animal "pump" air with its body, "the abdomen is flattened, as if the animal inspires: then the spinal column is curved, bent ventrally and this action is repeated several times". Eloff suggests that a break in the tunnel might be detected in this way, through the displacement of a volume of air.

The ranges of the three genera of blesmols found in East Africa scarcely overlap at all, except perhaps in very marginal habitats. The most widespread is *Heliophobius*, which occurs over the greater part of Tanzania and southern Kenya. *Cryptomys* is essentially an animal of relatively moist habitats, where droughts are not prolonged. *Heterocephalus* is very specifically adapted to the semi-desert conditions of the Horn of Africa.

In all the bathyergids the enormous incisors act as digging spades as well as gnawers of food. For none of them are the forelegs the only means of digging, as for the moles and the golden moles and the development of the forelegs is least pronounced in the blesmols. For them digging is mostly a seasonal activity, which is carried out when the soil is relatively soft or moist, so that their teeth are more than adequate to loosen the earth. The forelegs merely shuffle the earth back to be trampled and pushed by the hindlegs, which act as very mobile tamping bats, sometimes working in concert with the short, bristle-fringed tail. Having a different function from the forelegs, the structure of the blesmols' hindlegs has diverged. The normal vertical flattening of the claws is adapted to take stress in that plane and the mild fore-aft scratching of the forelegs maintains this structure on the digits of those

Cryptomys mechowii :
forelegs left,
hindlegs right.



limbs. The hindlegs have instead elongated and horizontally flattened "finger-nails" to enhance the shovelling and tamping action (see drawing, opposite page). Parsons (1896) pointed out that the *flexor digitorum longis* in the hindleg is peculiarly long and is separate from the *flexor hallucis longis*; this gives great mobility to the limb.

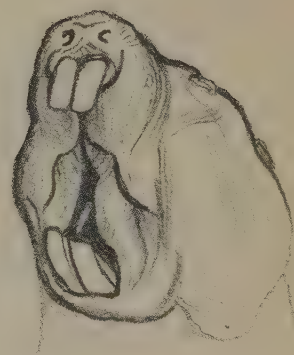
The "digging season" is a period of feverish activity for the blesmols and there is almost daily evidence of their burrowing in the form of new mole hills. These generally mark the end of short side tunnels off the main line burrow.

All blesmols use their hindlegs and rump to move soil but the load of earth ejected by the animal onto the mole hill varies. The highly social *Heterocephalus* kicks out a small shower of loose earth, which has been shovelled down the tunnel by a chain of workers. *Cryptomys* on the other hand, forces out a solid plug of moist earth. The movement of this bolus requires great effort: the animal bunches up against the earth, wedges its teeth and nose in the roof or sides of the burrow and then extends the body backwards in a single forceful heave, thus progressing down the tunnel in a series of short jerks. After throwing out the load the animal makes a rapid tattoo with the hindlegs which compacts the soil under the mole hill; sometimes it turns round and rams it with the snout. Jarvis and Sale measured 0.4 cubic metres of earth displaced by a *Heterocephalus* burrow system.

Unless already crushed and exposed, food is only recognized by touch, so that tunnelling must function as a random harvesting technique, without any sensory detection device beyond the crudest one of actual contact. Their food supply is an abundant one, even in very arid habitats and there is very little competition, except perhaps that of some type of insect larvae and pigs.

Experiments in captivity have shown that blesmols adapt easily to a variety of foods, but that they ignore anything smaller than can be easily manipulated by their forepaws or pared by their incisors. They are, therefore, rather indiscriminate root eaters, in spite of exhibiting strong local preferences for particular plants. Where a vast natural resource, such as roots, exists without being exploited, even the crudest harvesting technique will provide a living for the pioneer, but a random harvest of roots will only support a limited number of blesmols. The moment numbers rise to the point where an animal is digging fruitlessly, or the roots cease to renew themselves, ecological equilibrium is lost.

Roberts knew of places in South Africa where *Cryptomys* colonies had remained for 18 years (Shortridge, 1934). Genelly (1965) thinks that colonies of *Cryptomys* in Rhodesia eliminate their food plants in about 3 years and then move on. Watson (1950) reported that *Cryptomys* in Karamoja remain in one small area for "a number of years". Searching for *Heliophobius* on the Kapiti Plains, where they were very numerous at the turn of the century, McKay (personal communication) found that they were distinctly rare in the early sixties. These observations confirm that populations can be very unstable, but they also suggest that blesmols may be capable of achieving a state of equilibrium with their environment; this they do by not always killing the plant that feeds them and by sometimes using it as a living store. Extrapolating from *Cryptomys*, which stores roots, Jarvis (1969) suggested that the breeding individuals and juveniles of *Heterocephalus* depend on stores of food during



the dry season and that breeding seasons might be missed in years of low rainfall, but these suggestions were not confirmed by her subsequent observations.

Shortridge (1934) reported that *Cryptomys* hibernate or become partly inactive during the colder months of the South African winter. Although there seems to be a complete cessation of mound building during the dry season, activity is betrayed by the presence of much earth in the side tunnels, and aestivation seems unlikely in East Africa.

Most Bathyergids use part of their burrow system as latrines, but De Graaf (1962) has found faeces in *Cryptomys* nests; this is a typical feature of *Tachyoryctes* nests but is not found in those of *Heterocephalus* or *Heliophobius*.

All Bathyergids sleep in lined nest chambers. *Heterocephalus* and *Cryptomys* are social, *Heliophobius* is solitary. Breeding is probably seasonal.

Blesmol (*Cryptomys*)

Family Bathyergidae
Order Rodentia

Species

Cryptomys hottentotus
Cryptomys ochraceocinereus
Cryptomys mechowii

Local names

Fuko (Kiswahili), Ifuku
(Kinyakyusa, Kinyika), Enyukunyuk
(Ateso, Karamojong)

Measurements

head and body

135—201 mm

Cryptomys ochraceocinereus

tail 11—17 mm

weight 200 g

head and body

130—170 mm

Cryptomys hottentotus

tail 10—23 mm

head and body

180—215 mm

Cryptomys mechowii

tail 15—20 mm

Blesmol (*Cryptomys*)

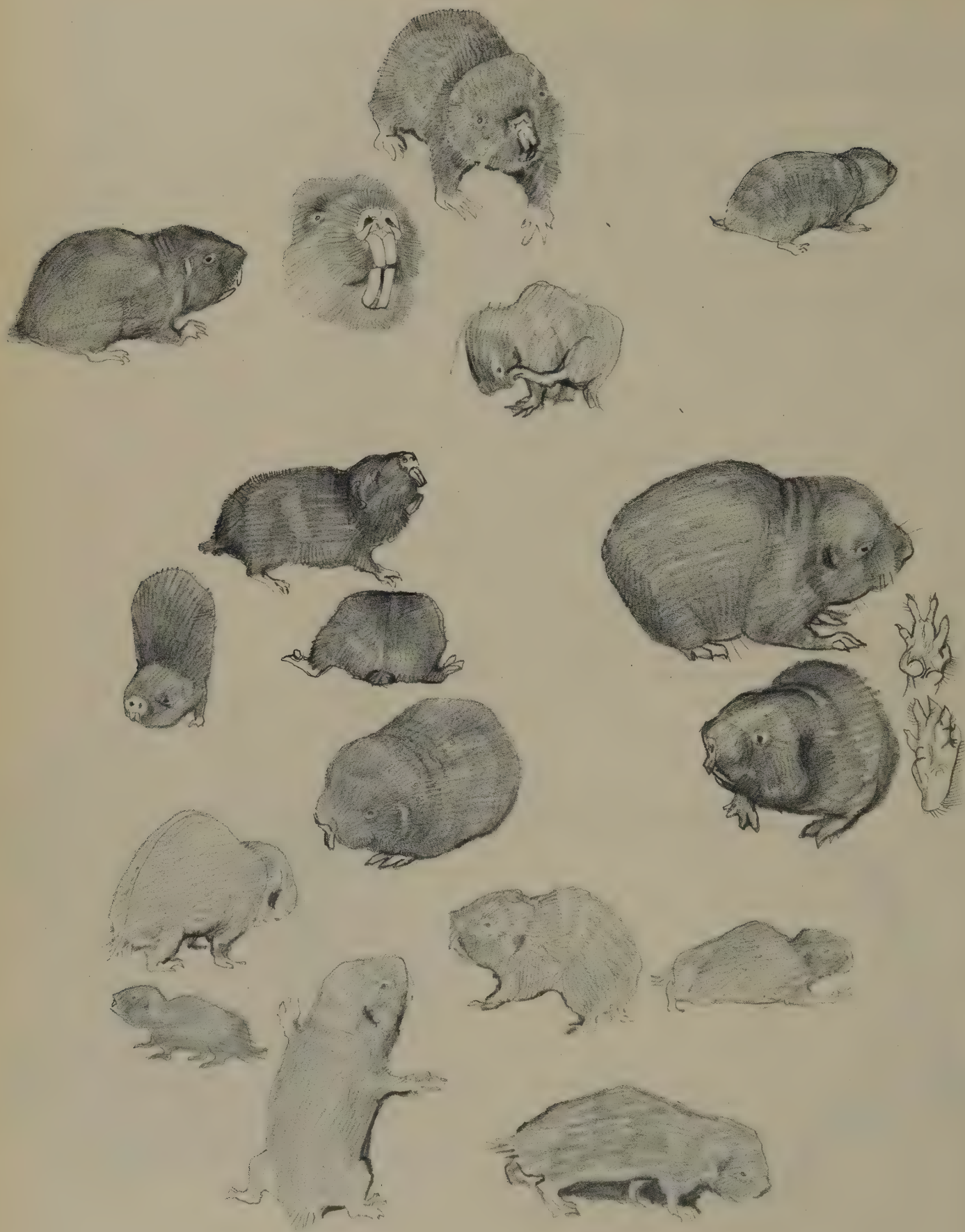
The two smaller forms represented in East Africa might be regarded with some justification as one species, particularly considering the great individual variation to which the members of this genus are subject. The giant blesmol, *C. mehowi*, only just enters East Africa in southern Ufipa, Tanzania. This giant species is sympatric with *C. hottentotus* over part of its range.

Cryptomys mehowi is a little known form of reportedly solitary habits and the following account only concerns the common blesmol, represented by *C. ochraceocinereus* in the northern savannas and *C. hottentotus* in the south.

These blesmols are short, velvety-furred animals with very prominent white teeth. The ears are scarcely visible and the blind eyes are of a bluish colour. In experiments, Eloff (1951a) has shown that the cornea of the eye is sensitive to air currents. This peculiar change of function probably explains why the eyes have not got lost in the fur. The long-clawed feet and the short tail are fringed with stiff hairs, which extend their surface area and enhance their performance in acting as light shovels of loose earth.

Outside the forest and desert zones blesmols are widely distributed in Africa. However, their distribution is discontinuous and there seems to be no overlap between *Cryptomys* and *Tachyoryctes*. In the East African part of its range, *C. hottentotus* seems to be a medium and high altitude species (up to 2,200 m) with a discontinuous distribution extending north to about 4° south of the Equator. North of this latitude the equivalent upland is occupied by *Tachyoryctes*. In effect, the latter genus is interposed between *C. hottentotus* and the northern *C. ochraceocinereus*. The related *Heliophobius* occupies the lower lying areas of East Africa.





Cryptomys occur in a wide variety of soils, in woodland, savanna and in secondary growth following the felling of montane forest. They adapt the depth of their tunnels to the consistency of the soil and on seasonally flooded ground they even throw up extensive mounds, in which a living chamber and foodstores are above the high water mark. Watson (1950) found *C. ochraceocinereus* very local in Karamoja, favouring deep soils in the neighbourhood of rocky hills.

Food supply is probably a most important determinant of their presence as they seem to be rather specialized feeders and their foods do not appear to grow on soils of low fertility. In the Garamba *C. ochraceocinereus* feeds mostly on the woody roots of a type of wild yam, *Dioscorea abyssinica* (Verheyen and Verschuren, 1966). In Rhodesia, *C. hottentotus* feeds very largely on the bulbous bases of black seed grass, *Alloteropsis semialata*. Other roots or bulbs listed by Genelly (1965) are *Scleria*, *Homeria* and *Moraea*. *Cryptomys* are a common pest in flower and vegetable gardens with a special taste for the bulbs or roots of cannas, dahlias, artichokes, carrots, groundnuts and potatoes. They also eat the base of young sisal plants and aloe leaves. Worms, termites and cockchafers' grubs have also been recorded from stomachs.

Food gathering is a seasonal affair for *Cryptomys*. The animals are busy in the rainy season extending their burrows to new feeding areas. Genelly measured one colony as digging 135 metres in one month. They carry roots and bulbs to their stores, which are short chambers that may be quite close to the feeding areas. In the dry season, they do not make mounds but, instead, redistribute soil into old disused tunnels. The food is not harvested entirely below the ground and Watson (1950) has reported them digging up newly sprouted grain over a wide area and being trapped on the surface many metres from the nearest mole hill. Also their nests and stores sometimes contain leaves which must have been gathered above ground.

Roberts observed that

"although the animals dislike getting wet, they are often found in marshy ground where their food is to be found in plenty, the tunnels then leading to higher ground such as mounds or hillsides, where the bulbs can be stored in dry ground. . . . They are very local in my experience, seldom going far from certain spots, doubtless where certain bulbs or roots are always to be found, but not necessarily, as one might expect, where the soil is loose or sandy, very often remaining in the stoniest and hardest ground. I have known these animals remain eighteen years in certain places on rock kopjes". (In Shortridge, 1934.)

Food is not found by scent, except at very close quarters. Eloff experimented with imitation bulbs made of plaster and found the blesmol was deceived. The animals were extraordinarily sensitive to vibrations and tactile sensations felt through the vibrissae on the face.

The vibrissae and the cornea of the eyes are also very sensitive to any air current and the animal will often hasten to repair any break in the ceiling of the burrow, when some heavy animal or rain has opened it up. When rain floods out the burrow, blesmols come to the surface, where they are extremely vulnerable if there is no cover. It is rare, however, to find them in this predicament. Roberts thought they preferred to dig while the earth was warm, but this might be an activity pattern typical of colder latitudes. It is not true in Karamoja.

◀ *C. hottentotus*.

The blesmols' capacity to find their way about in laboratory mazes has been tested by Eloff. Quite unexpectedly, he found the males decidedly superior in this to the females, a finding that suggests that there may be some division of labour within a colony. Roberts (1951) observed that the younger animals were usually the first to be trapped "but when the traps are left in the same places for several days thereafter, the older animals are often caught; this suggests that the older animals drive out the younger ones to forage and bring back food to the storage chamber".

The social structure of a *Cryptomys* colony is probably subject to cycles that follow the annual seasons, as well as to a longer cycle of population build-up followed by dispersal and decline.

Being root eaters, blesmols naturally tend to have a marked influence upon the vegetation and more particularly on the abundance of their own food plants. Once the numbers of blesmols have built up in an area, they eventually face a shortage of food. If the area that has been used by a small population is adjacent to new unused areas, the natural process of burrow extension during the rains might allow a sort of land rotation to be practiced. Even so, the establishment of a new burrow system and new feeding areas must be attended by numerous hazards and a drop in numbers could be expected every time the colony moves. Where blesmol colonies have proliferated over a large area, they face an inevitable population decline once they have used up their food resources.

There is casual evidence that both these processes occur but they have not been the subject of systematic study and an investigation of the population dynamics of blesmols would be very interesting.

Watson (1950) observed that, if a local population is undisturbed, it will remain in one area for a number of years. Genelly, in an eight months' study, was able to say that a colony of ten or twelve animals tended to use up its food plants in three years and then moved on. In one cultivated valley in south-western Tanzania, I have noticed a general tendency for molehills of *C. hottentotus* to become numerous for a year or two; this is followed by a few years of scarcity and then another of increase. This casual observation implies general fluctuations of populations over a relatively large area.

Colonies of animals share a simple burrow system, which extends over about 300 sq. metres. Between two and twelve animals have been recorded sharing the system and sleeping in the communal nest, which is lined with grass, root debris and leaves.

G. de Graaf (1961) excavated a nest that was made of vegetable matter, weighing about 240 g and measuring some 26 cm in diameter; it was soiled with faeces and infested with mites. The nest is built by several animals and is often betrayed by the extensive earthworks near it, the mounds containing more earth than that thrown up from the feeding burrows.

The methods of digging and handling earth are rather similar in all bathyergids and were described earlier.

Cryptomys utter a variety of squeaks and grunts; they also make a low growling noise, which is possibly a threat. They dislike rain and mud and try to groom it off at once when soiled; their short velvety coat is well adapted to repelling dirt and being easily cleaned.

Their burrows are shared by a species of frog, *Kassina senegalensis*, which feeds on various invertebrates falling into the burrows. In this way, a commensal makes use of the burrow system as a food trap, very much as the insectivorous moles do. This frog also lives in termitaries, but is essentially a subterranean species.

Cryptomys are eaten in some areas and are often trapped or dug out by small boys in the villages. Various carnivores, particularly *Poecilogale* and serval cats, hunt them and they have been found in the stomachs of snakes and in the pellets of owls (Davis, 1959).

They are very hardy animals and are well suited to laboratory study. They will use artificially constructed subterranean burrows built against a glass observation panel.

Their parasites consist mainly of mites, which Bateman reports clustering round the lips of the newly born.

The gestation period is not known. They probably breed once a year during the rains. Genelly's intensive study, running over eight months, missed all evidence of breeding behaviour. A female in Karamoja was collected with embryos in December. The female has two pectoral and one or two inguinal pairs of mammae. She gives birth to one to five young.



**Silky Blesmol,
Silver Blesmol**
(*Heliophobius
argenteocinereus*)

**Family
Order**

Bathyergidae
Rodentia

**Measurements
head and body**

155 (100—200) mm

tail

15—40 mm

weight

160 (142—168) g

Silky Blesmol, Silver Blesmol (*Heliophobius argenteocinereus*)

The silky blesmol is a long-haired grey animal with prominent white incisors. The full dentition numbers six cheek teeth for each jaw, but the anterior premolars are usually shed before the last molars have emerged. The palate is exceptionally narrow.

In a somewhat variable species, seven described races may not have very much validity, but a population east of Kilimanjaro does seem to be distinguishable on the basis of warmer colouring and a slightly different conformation of the palate. This blesmol has been called *Heliophobius spalax*, but is almost certainly no more than a local race of *H. argenteocinereus* as there is no evidence of sympatry.



The silky blesmols are distributed over most of eastern and central Africa,

but do not occur in Uganda or northern Kenya. They occupy drier and warmer habitats and lower altitudes (750—1,500 m, under a rainfall of between 250—600 mm a year) than *Cryptomys hottentotus*. In parts of the Southern Highlands, the two species are separated by altitude rather than distance and, although small scale maps cannot bring out the differences in ecology, their habitats are quite distinct. *Heliophobius* can withstand a long dry season and favours well-drained, sandy soils on rocky hillsides on open plains or in *Combretum* or *Brachystegia* woodland.

Food plants are probably the major factor in determining the local abundance and distribution of *Heliophobius*; these consist mainly of tubers and bulbs. On the Athi Plains, Jarvis and Sale (1971) recorded *Dolichos* and *Vigna* species as the principal foods. The tubers of these plants grow at a depth of about 20 cm and most of the foraging burrows are at this depth. *Heliophobius* does not feed on the surface, although it must occasionally emerge to collect grass to line its nest and skulls of this species have been found in owl pellets.

Well compacted and very firm earth seals against enemies and rain are made in the burrows of this species. These burrows are dug in similar fashion to those of the other blesmols and the long fur of *Heliophobius* does not appear to be an obstacle to its bulldozing earth backwards along the burrow. The average length of 4 burrows measured by Jarvis and Sale in Kenya was 47 metres. These authors found nothing approximating a store and only saw a few small bulbs in the nest chamber. They discovered bolt holes, that went down 46—54 cm and which were used by the animal whenever danger threatened, but which were very difficult to find because the animal blocked them with earth after entering the burrow.

When kept together in captivity these animals are very aggressive and fight one another whenever they meet. In the wild the burrow systems are occupied for much of the year by single animals. Their behaviour during the breeding season should, therefore, be very interesting.

Jarvis and Sale dug out and mapped three closely situated burrow systems on the Athi Plains, each of which was occupied by a subadult animal. The

“three systems were adjacent to each other and each contained a subadult animal: since each animal weighed approximately 80 g it is probable that they were siblings. Study of these three burrow systems and the presence of old mole-hills in the ground between them strongly suggests that the three burrows were originally part of one system. The connecting burrows were probably plugged when the young animals became independent. No trace of the mother was found, she had either died or moved to a neighbouring area.”

Heller collected females with 2—3 embryos at the end of May at Loita, but Copley (1950) says that they produce one litter a year at the beginning of the long rains. The young number between one and four per litter.

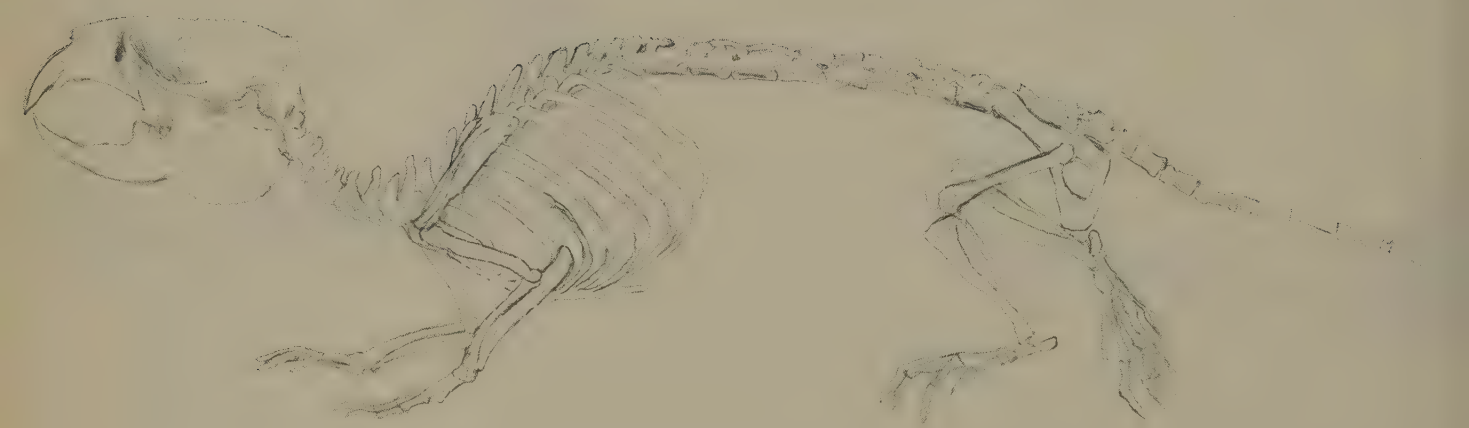
Sand-puppy, Naked Mole-rat (*Heterocephalus glaber*)



Sand-puppy is an appropriate name for this animal, as the first impression of it squirming in the sand is of a newly born or even foetal animal, feverishly wagging its tail—which is unusually long for a blesmol. The resemblance with an infant or embryo does not stop short at its naked skin and uncoordinated movements, for Hill *et al.* (1957) reported that the organization of its reproductive system also simulates an embryonic condition.

The sand-puppy has a poorer capacity for thermoregulation than any other known mammal (McNab, 1966). Other peculiarities are its uniquely structured kidneys, a degenerate gut with no colic loops and the absence of sweat glands.

A Lower Pleistocene fossil, *Heterocephalus quenstedti*, has been found at Laetolil and another *Heterocephalus* at Olduvai. These fossils suggest a southerly extension of the semi-arid conditions of the Horn of Africa in the early Pleistocene, for *Heterocephalus* is an animal exclusively adapted to arid



**Sand-puppy,
Naked Mole-rat
(*Heterocephalus
glaber*)**

**Family
Order**

Bathyergidae
Rodentia

**Measurements
head and body**

80—92 mm

tail

28—44 mm

weight

30—80 g

conditions, and which is limited today to Somalia, eastern Ethiopia and northern Kenya; it is a reliable "indicator species" for arid conditions. This genus has also been found in Miocene deposits at Napak (Bishop, 1962); this is a doubly interesting discovery, because it shows the great age of the Bathyergidae and also because it suggests that relatively dry conditions existed at this site in the Miocene, even supposing that at such an early date the genus might have been less exclusively a desert animal than it is today.



Heterocephalus live in a variety of soils and make their burrows at several levels down to a maximum depth of less than one metre, so that there is some choice of temperature range within one burrow system. There is a large nest chamber lined with the dried peel of roots and root hairs and above the nest there is a complex network of tunnels, with food-gathering galleries radiating out 30 to 40 metres from the centre. Volcano-shaped mole-hills are clustered round the nest, with a scattering of hills also along and above the outer tunnels and solid plugs are made at the base of these mounds. The burrow system of a single colony of *Heterocephalus* is more extensive than that of any other mole-rat species; this is due partly to the concerted digging of the numerous animals in the colony and partly to a dispersed food supply.

The burrow atmosphere, when measured by McNab, was nearly saturated at all hours. The animals' nakedness ensures that they keep cool, for a coat of fur would slow down heat loss, which is also further slowed down by

an atmosphere that inhibits evaporation. McNab has found that the naked mole-rat's rate of heat production is less than half the normal one for an animal of its size, while the rate of heat loss is nearly three times as great as expected; a loss that is assisted by a high peripheral circulation.

This peculiar heat-budget is reflected in *Heterocephalus*' very low body temperature—about 32°C—which makes the animal very vulnerable to cold and entirely dependent on a stable environment.

Sand-puppies appear to be most content at a temperature of about 30°C, which is the day and night average temperature within the burrow, although the outside temperature can vary from 5 °C to 45 °C. They are very susceptible to cold and lose all coordination when subjected to a steep drop in temperature.

Laboratory experiments suggest that sand-puppies have a catholic taste as far as roots and other vegetables are concerned. They are known to eat the vine, *Cissus aphyllantha*, the roots of *Acacia*, *Commiphora*, *Balanites*, *Boscia*, *Erythrina* species and the bulbs of *Ammocharis*, *Berkheya* and *Indigofera*.

Jarvis (1969) suggested that stores played an important role in the biology of this species but subsequent observation has not revealed the presence of stores.

“Not infrequently tubers (*Vigna* sp.) were found lying partly exposed in the burrows. The tap roots of these tubers were always undisturbed and the plants were viable and seemingly unaffected by the exposure. Many of these tubers were partly eaten by the mole-rats but this again did not kill the plants and a number of quite extensively eaten tubers were sprouting healthily. *Heterocephalus*, like *Heliophobius* appear to visit tubers growing *in situ* and eat enough to satisfy their hunger. Small sections of the epidermis are removed from the tuber and the mole-rats then hollow out the centre leaving the rest of the epidermis intact.

Storage of tubers in special chambers does not normally occur but small combs like those from the sedge *Mariscus* appear to be carried to the nest and eaten there.

The presence of tubers appeared to induce branching of the tunnels in the immediate vicinity of the find. This is particularly noticeable in the relatively unbranched linking burrows where many of the branches that did exist were associated with one or two tubers. An extra rich area of tubers may produce a maze of tunnels, many tuberous plants propagate by vegetative reproduction and tend to occur in clumps, this may well be the reason behind the development of this tunnel branching behaviour in *Heterocephalus*”. (Jarvis and Sale, 1971.)

Like hares and rabbits, *Heterocephalus* circulate their food twice (coprophagy). They lie on their backs in order to swallow the soft primary pellets. The dry secondary ones are dropped haphazardly in the burrow, but not in the nest. When feeding, the animal holds the root in its forepaws and chews up and down, rapidly consuming the root until the piece that is left is too small to hold firmly, whereupon it is discarded.

Sand-puppies squabble over food in captivity, particularly if a favourite item is in short supply. The largest and most energetic animal usually wins the food amidst much violent squealing and head shaking, but the animals do not bite one another. When excited, they flush a reddish-violet colour.

Like all blesmols, sand-puppies sustain long periods of intense activity. The hindlegs kick out the dry earth from the exit hole with great force,

creating a circle of piled earth or sand, like a volcano. During the wet season, similar jets of watery mud are shot out of the burrow. The tail and the forelegs function as a tripod, while the hindlegs are kicking; but the tail appears also to act as a sensory probe, or stout antenna, when the animal travels backwards down a tunnel; it wags rapidly from side to side. The digging chain has been described and illustrated by Jarvis and Sale (1971):

"One mole rat digs at the earth face and kicks the soil to the animal standing just behind it. This animal is the first member of a chain extending along the burrow. On receiving the earth the mole-rat begins moving back along the burrow with its load. It pushes the soil to the side branch leading to the surface where it is collected by a mole-rat responsible for the final disposal of earth. The animal then returns to the working face by straddling the earth-moving mole-rats and gradually working its way forwards. In this way a constant chain of mole-rats is formed; the forward moving ones straddling the backwards moving earth-laden animals and working their way to the front where they again collect a load of soil and begin the backward journey to the surface".

Tunnels are mostly constructed during the rains and all animals participate in the tunnelling. They are occasionally flooded out in spite of blocking up their tunnels. A colony generally ranges from one pair to about 30 individuals, although Thomas (1902) records colonies of 50—100 animals in Somalia. Colonies may be separated by extensive areas of unsuitable ground, but where conditions are right and there is abundant food, the colonies may be less than a hundred metres apart. Stark found that about 20 to 30 animals lived in an area of 1,000 sq. metres. Hill *et al.* (1957) introduced a single animal into an established colony. The newcomer, which had been rather quiet and inactive on its own, became very excited, nuzzling, rubbing and following other animals; it remained extraordinarily active for some days. The same authors reported that their field-workers had observed the "assimilation" of colonies.

Like other blesmols, *Heterocephalus*, are preyed upon by small carnivores, raptorial birds and snakes.

At higher altitudes, the range of *Heterocephalus* overlaps that of *Tachyoryctes*. For instance, both animals are found at Moyale, but the habitat is probably marginal for both species in such areas. A green beetle, *Asolemus phoebius*, which was first discovered in a mole-rat's nest, is a common inhabitant of their runs and a toad, *Pyxicephalus*, inhabits their burrows.

In some arid areas sand-puppies have a useful ecological role; they are active just before the rains and, from the point of view of forestry and pasture, this may be a good thing: their burrowing does at least allow water to percolate to greater depths.

"In the Erigaro firewood reserve, which prior to conservation was sparsely covered in vegetation and badly eroded, very little percolation was possible. Bunds were constructed and there *Heterocephalus* appeared to make his home, making the bottom of the bunds appear quite honeycombed with holes. The bottom of the bunds, after one year, is now well covered with grass and young regenerating acacias". (Tribe in Hill, 1957.)

Reproduction has not been studied. Jarvis (1969) records the birth of a litter of five *Heterocephalus* on the 7th of April and the capture of two juveniles also in April. Hill *et al.* record two pregnant females in May.

Heterocephalus' testes are abdominal and the sexual condition is not visible externally. An adult has been seen carrying a squeaking juvenile in its mouth. The young weigh about 2 g at birth and look even more foetal than the parents.



Root-rats

Rhizomyidae

The history and the relationships of *Tachyoryctes* are not certain, but most modern workers have followed Grassé in placing it in the Rhizomyidae.

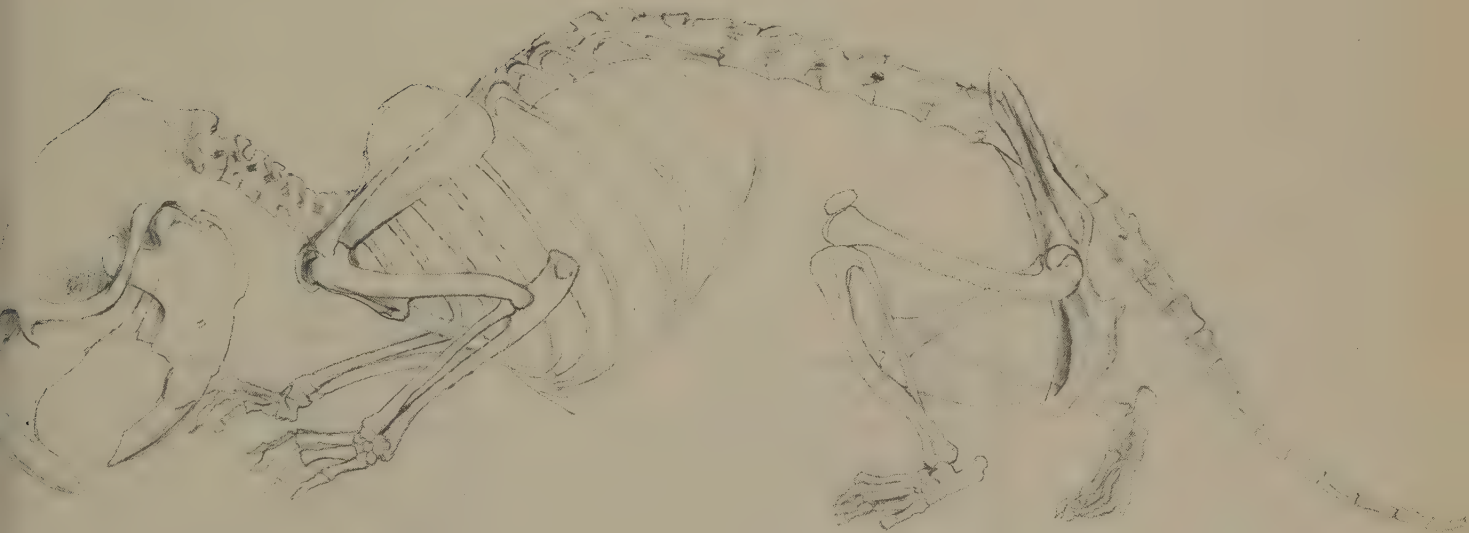
This family is represented by three living genera, two of which are Oriental and the third is the African *Tachyoryctes*. Of very uncertain relationship is the Malagasy *Brachyuromys*.

The earliest fossil rhizomyid is *Tachyoryctoides* from the Asian Oligocene. Other Eurasian fossils are known from the Upper Miocene. Rhizomyids retain eyesight, small ears and a rat-like tail, betraying their more recent myomorph origins. They probably share a common ancestry with the cricetids.

The living root-rat, *Tachyoryctes splendens*, is known from the Lower Pleistocene at Laetolil and there are earlier fossils of rhizomyids in Africa. It is possible that the ancestral stock of *Tachyoryctes* came into Africa at a relatively late date, perhaps in the late Miocene or Pliocene and that their invasion has tended to be limited by the bathyergids, which are much more highly specialized.

The success of *Tachyoryctes* in favourable habitats is demonstrated by the abundance of their mole-hills, a success that might be partly due to the catholicity of their diet of herbs and grass.

This species' dominant position and its apparent replacement of *Cryptomys* was discussed earlier.





Root-rat
(*Tachyoryctes*
***splendens*)**

Family
Order
Local names

Nadunach (Tepes), Fuko
(Kiswahili), Bumo ongwet (Sebei),
Unungwet (Kimasai), Pumgumwa
(Suk)

Rhizomyidae
Rodentia

Measurements
head and body

195, 202 mm (male averages)
178, 194 mm (female averages)
160—260 mm (range)

tail

66 (50—95) mm

weight

206, 250 g (male averages)
175, 218 g (female averages)
160—280 g (range)

Root-rat (*Tachyoryctes splendens*)

Root-rats are immediately recognizable by their prominent orange teeth. Their coats are very soft and thick, usually some shades of russet in colour but with a dark grey undercoat showing when the hair is ruffled. Juveniles less than 4 months old are black. This colouring is also seen on some adult-sized animals but there is usually a period of about 3 months in which the adult brown colouring extends from the flanks over the whole body. Males are of a lighter colour than the females as well as being somewhat larger.

The average measurements given opposite are from two different populations, the western *ruandae* form (from Rahm, 1969) and the larger *ibeanus* form (from Jarvis and Sale, 1971) found near Nairobi. There seems to be little point in listing the very numerous forms that have been described, but it should be mentioned that the high altitude form on Mt Kenya is particularly large, and that the western Uganda forms show minor differences in skull structure.



They range over the uplands of northeastern Africa, from Ethiopia and parts of Somalia as far as the eastern Congo (Zaire), Ruanda, Burundi and northern Tanzania. They are seldom found in areas with less than 500 mm annual rainfall and flourish best in wet uplands. They can withstand great cold, living at 3,500 m on Mt Kenya. *Tachyoryctes* are very common on every mountainous massif in Kenya and over the uplifted floor of the Rift Valley between Baringo and Suswa. They are very numerous indeed in particular localities, such as the alluvial plains southwest of Lake Naivasha, in a narrow subalpine zone on Mt Kenya, on the Mau and in parts of Ankole and Kigezi. Such localities are characterized by deep fertile soils with a reasonable and well distributed rainfall. They favour open grassland, thinly treed upland savanna, moorland and cultivation, particularly where this has replaced forest. Although they occur on Ruwenzori, they do not seem to have acquired there the pre-eminence they have in equivalent habitats further east.

Tachyoryctes make relatively short tunnel systems, which run just below the level of the grass roots on which they feed; that is about 15—30 cm below the surface. In the dry season, however, they dig down as much as one metre and are very much less active (Rahm, 1971). This author measured temperatures in the burrows and found 18°C in the dry season and 20°—22°C in the wet season. Outside the burrow the temperature at night can go down to 11°C. Great differences in temperature are discernible in the nests; this is because the dung and nesting material accumulate and form a rich compost, which generates heat in wet weather but dries out in dry weather. The compost is constantly being added to with more dung and nesting material, the latter being augmented with debris from the feeding store. In the very cold alpine zone of Mt Kenya, nest temperatures can be as high as 12°C, while the soil temperature is 5°—7°C (Coe, in Jarvis and Sale, 1971). These authors report that on Mt Kenya

“The distribution of mole-rats in many mountain valleys is associated with large symmetrical mounds, up to 6 m in diameter, covered with *Alchemilla* sp. Many of these raised areas are occupied by *Tachyoryctes* and Coe (1969) believes that these mounds are directly attributable to long periods of mole-rat activity below. It is however possible that the mounds were produced by some other factor and because they are raised and therefore better drained are colonized by *Tachyoryctes* and other rodents. This problem has its parallel in the much debated question as to whether pocket gophers originated the ‘mima-mounds’ of the western United States, or whether they can be attributed to natural forces such as wind, water and ice”.

These authors also found that females dug more extensive burrows (34—44 m) to the males (14—34 m). This range of tunnel lengths is similar to those measured by Rahm (1971). Both papers illustrate plans of typical burrow systems.

Root-rats come to the surface much more than blesmols do and they are sometimes found run over on roads. Apart from collecting grass for their nests they forage for food, particularly in cultivation, where they will damage beans and peas as well as pyrethrum roots, groundnuts and root crops. They also “graze” to some extent, as fresh grass can sometimes be found in their stomachs and in their tunnels. However, roots are their main diet and Rahm lists 21 species of plants, the roots and tubers of which are eaten by *Tachyoryctes*. Rahm has reported that food is stored for the dry season. The roots



are collected to one side of the nest and as the quantities of debris and nesting material increase, the nest is extended and enlarged, during which process some roots may be buried in the compost.

The digging technique of the root-rats is quite different from that of the blasmols; the root-rat is reluctant to move backwards and after gnawing and loosening a quantity of earth and shovelling it behind, it turns round and pushes it with the chest and the side of its face with some assistance from the forelegs. The animal also seals its burrow against the elements and intruders with a well-packed earth plug. Each burrow has a bolt hole that is usually near the nest and goes deep into the ground; Jarvis and Sale recorded a depth of 178 cm. The mole-hills are large piles of subsoil. Small ones marked by a broken earth plug reveal spots where the animals have come up to forage on the surface.

The captive root-rats I kept slept all day and chewed throughout most of the night with peak spells of activity between 6—9 p.m. and 5—7 a.m.

They are very sensitive to noises, starting at any sudden sound. They see objects within the range of a few feet. Although they will scurry about quite rapidly inside an earth-filled box and will disappear down a burrow with dispatch, they are clumsy and inept out in the open, threatening with their orange incisors and squealing when molested. They fight savagely with each other over food, but if an animal is feeding quietly it appears to warn an approaching animal by clicking its teeth.

Although densities of root-rats can be astonishingly high, each animal lives in a self-contained burrow. Rahm gives some indication of how solitary these animals are with figures for a plot of 7,200 sq. m where some 49 animals were excavated (about one for every 140 sq. m). All these animals were living alone in their own burrows, except for a pair found together. Presumably a female in oestrus tolerates the temporary invasion of her burrow, or perhaps she visits that of a neighbouring male; at any rate, this brief contact is a departure from the usual solitary state. In this plot Rahm found an equal sex ratio and about half as many young animals as adults, implying that the population turnover must be fast. He found that over the year 100% of the females were pregnant, but that the percentages followed a very steady curve

from about 2% at the end of the dry season to about 20% at the end of the rains. As animals become adult and capable of breeding at 6 months, the average life expectancy of a root-rat must be about 1 year. It is possible that disease may occasionally control numbers, as Heller found several dead animals, but Rahm does not mention this as a significant factor in his study of over ten thousand animals.

The enemies of root-rats are mostly small carnivores, particularly the zorilla, *Ictonyx*, and the striped weasel, *Poecilogale*. The latter animal has been seen to enter and follow the burrows (Rahm, 1971). The serval cat, *Felis serval*, has also been seen sitting near a mole-hill and leaping into the air to drop onto a rat when it surfaced. Eagles, augur-buzzards and owls also feed on root-rats. Stockley describes an eagle owl, *Bubo lacteus*, hunting root-rats in Kenya:

“At 5,000—6,000 feet it takes great toll of various root-rats. These are very destructive in the farmers’ fields, notably those of pyrethrum, and the owl can spot a mole-rat working underground and drop on it, pushing its great talons through the earth to grab its prey”.

Root-rats can be a nuisance in cultivation, and they were once sufficiently common on the Jinja air-strip to cause bumpy landings. They used to be eaten in Kigezi, on Mt Elgon and on the Mau. In several areas they are forced to surface by the flooding of their burrows. In Buganda they are very rare, probably because they have a special value as charms. A purse made out of *Tachyoryctes* skin is thought to bring prosperity and is sometimes given to an extravagant man, perhaps in the hope he will keep his money therein, rather than spend it.

The burrows and particularly the nest of *Tachyoryctes* provide a home for numerous commensals including some blind species of beetle. Scarabid larvae are very common in the compost of the nest and Jarvis and Sale list isopods, dipterous larvae, pseudo-scorpions, mites and various beetles. *Otomys* also enter the burrows sometimes.

The breeding of root-rats has been the subject of interesting papers by Rahm (1969 and 1971), who examined nearly 10,000 females. He established that their gestation is 46 to 49 days and showed that pregnancies dropped to a minimum at the end of the rainy season. Thus the period of inactivity and retreat to deeper levels during the dry season has the effect of reducing contact and sexual behaviour; 58% of the females examined had one young, 37.9% had two, 2.2% had three and 1.1% had four. Foetal resorption has been noted in this species, generally serving to reduce the number of foetuses.

Rahm found that occasionally mothers killed and ate their newly born offspring in captivity. The young are born pink and naked but they have grown a fine coat at the end of one week and by the age of two weeks are black miniatures of their parents and very active. The black coat starts turning brown between two and three months of age, at which time the juvenile leaves the mother’s burrow. Most animals have a completely brown coat by the time they are six months old and ready to mate.



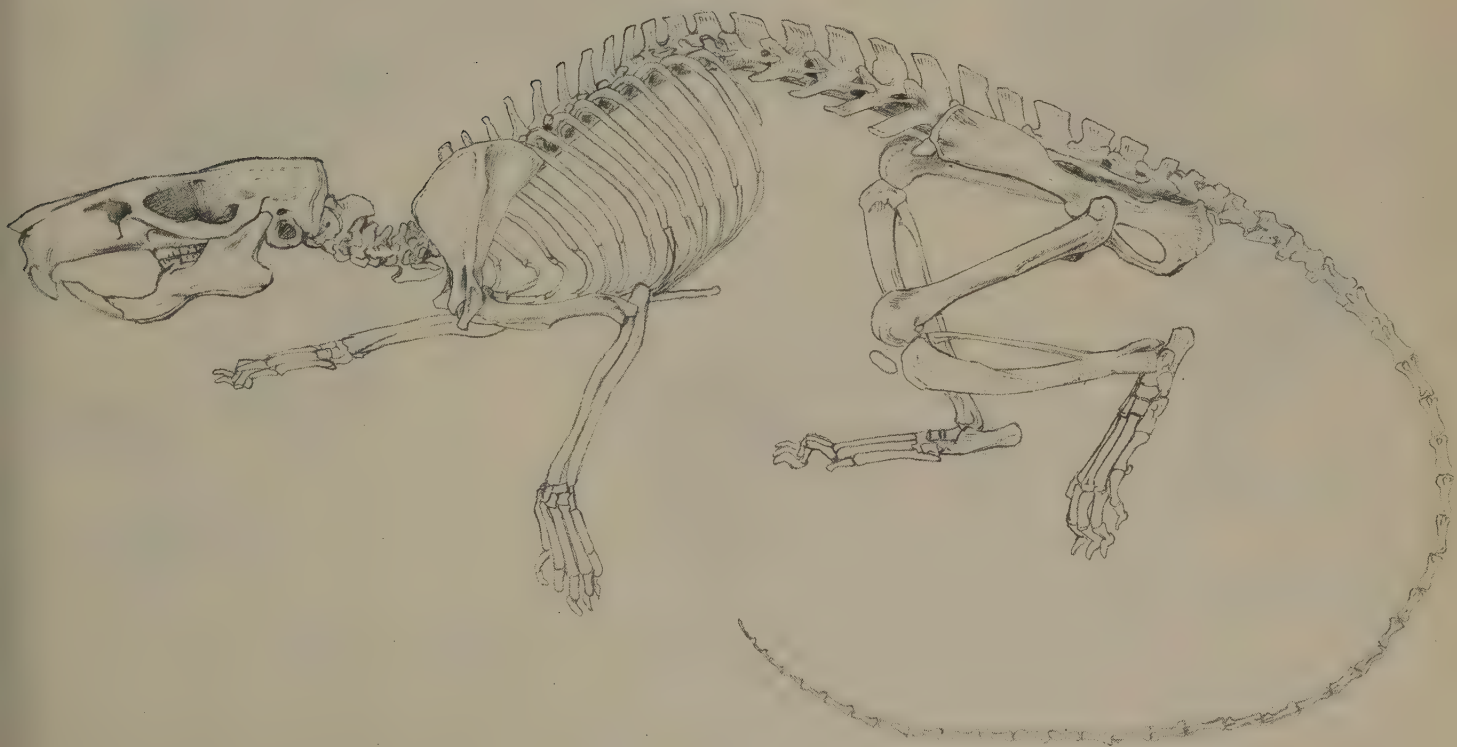
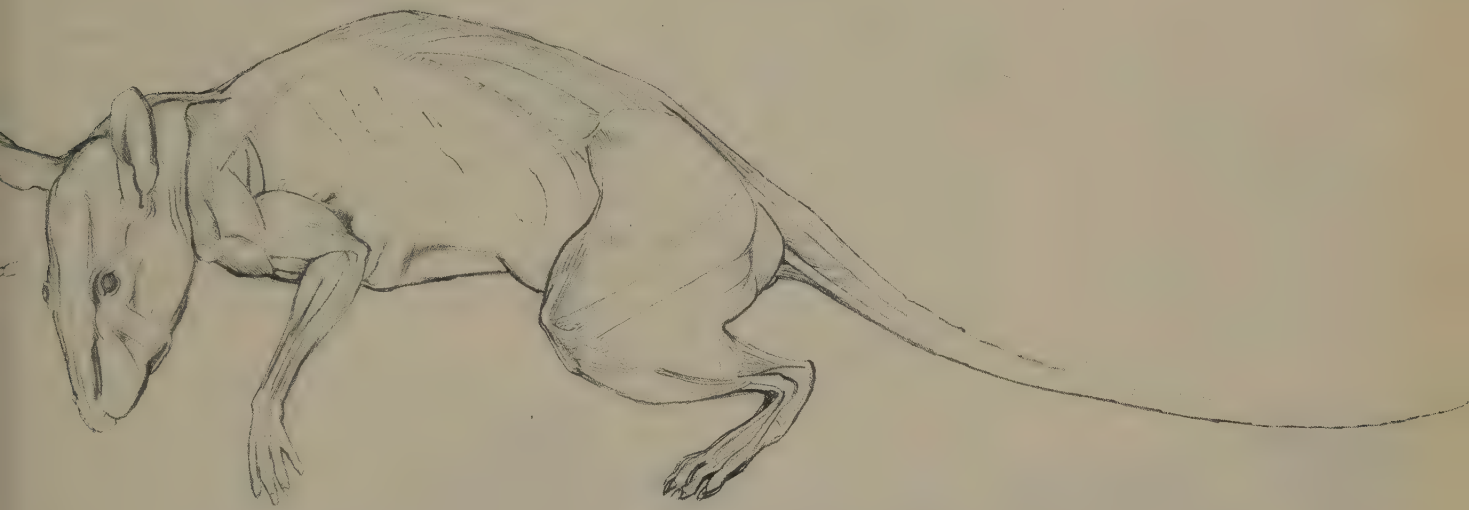
Myomorphs

Myomorpha

This suborder contains all the very numerous rat-like rodents. The usefulness of subdividing the rodents into three suborders has been questioned by several authorities.

The uncertain affinities of several African groups make it more realistic to classify the groups of rodents by families or at most by superfamilies.

Of the East African rodents two superfamilies have been placed in this suborder by Simpson (1945), the Muroidea and the Gliroidea.



Rat-like Rodents

MUROIDEA

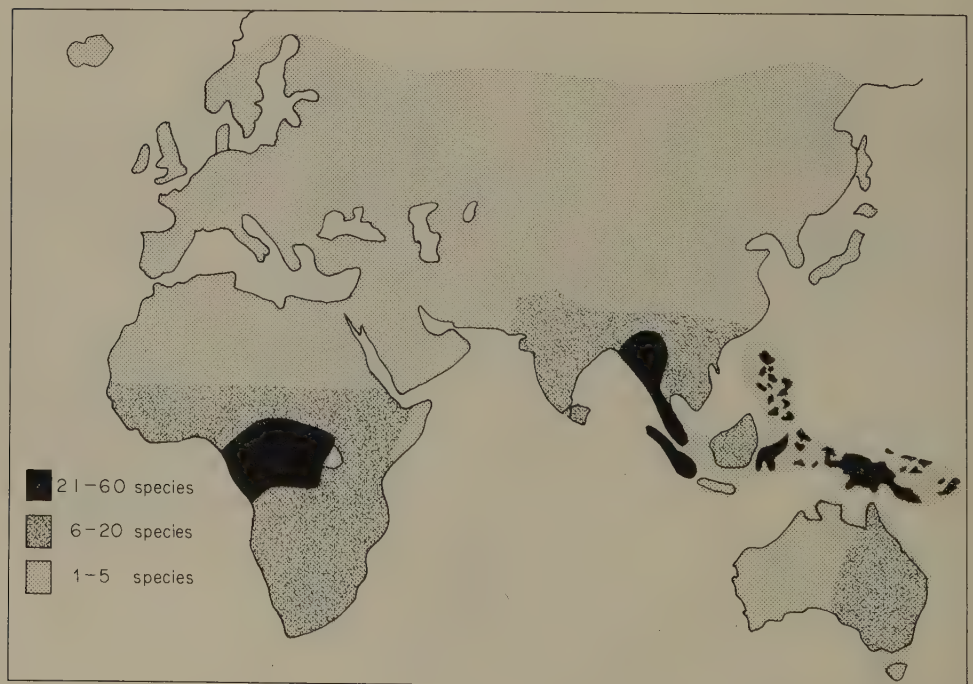
Rhizomyidae
Muridae
Cricetidae

Murinae
Gerbillinae
Lophiomyinae
Dendromurinae
Petromyscinae
Cricetomyinae
Otomyinae

Those rodent species that have more or less rat-like form are very numerous. There may even be difficulties in the field distinguishing members of different families; for instance, gerbils and climbing mice have strong resemblances to murid rats and mice that occupy similar niches.

Recognizing the convergences that occur I have devised a pictorial key (overleaf) which starts with the overall impression given by the animal in the field and then proceeds to the details that allow the family to be identified. For the museum worker this field key may be less useful but very adequate taxonomic keys already exist, e.g. Allen (1939), Ellerman (1940, 1941, 1949), Ellerman *et al.* (1953), Foster and Duff Mackay (1966) and the Smithsonian preliminary identification manual.

The overlapping of rather similar cricetid and murid rodents in Africa is very interesting. Several cricetids are rare and declining species—i.e. *Beamys* and *Delanymys*. There is also evidence that one species, *Deomys*, is competitively inferior to its murid equivalent (see p. 542). Other cricetids appear to avoid competition by being specialized in some way or other. The overall implication is that the murids are in the last stages of taking over from all but the most specialized cricetids.



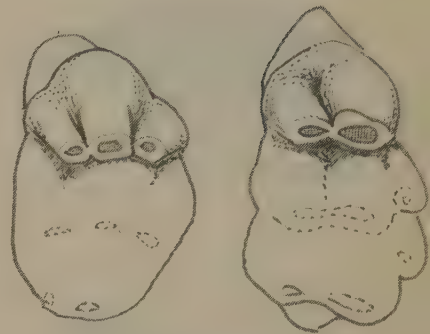
World distribution of Muridae.

The relationship of the murids to the cricetids is the subject of some disagreement. The controversy centres on the interpretation of how the murids developed their many-cusped molar teeth. Schaub (1938, 1958), Petter (1966a) and Lavocat (1962, 1967) believe that the murids developed out of cricetids, while Vanderbroek (1961, 1966) regards them as both having a common ancestor, while Misonne (1969) has developed the latter thesis and has suggested that the murids originated in southeast Asia with a secondary expansion and development in Africa, and that they have no connexion with the rather rat-like Dendromurinae and Cricetomyinae. This invasion of Africa probably took place in the late Miocene or Pliocene.

A broader dimension is given to Misonne's exposition by the definition of distinct ecological trends in four groups of African murids. These trends are discussed further in the profiles of the murids, which broadly support Misonne's position.

The most certain way of separating murids from cricetids is to examine the front of the first molar, where three cusps can generally be seen in all but the oldest animals while cricetids have only two.

The dental patterns of the Muridae and the subfamilies of the Cricetidae are illustrated in the profiles.



M¹ murid and cricetid



PICTORIAL KEY TO



Generalized rat or mouse-like forms with pointed faces, medium build, equal limbs, naked tail, short fur. Omnivorous.

M1 with 2 cusps in first toothrow.
Giant size (H. & B. 250—400 mm), p. 550.
Medium size (H. & B. 100—250 mm), p. 547.
Medium size, M1 with 3 cusps in first toothrow, p. 577.
Small size (H. & B. 50—100 mm), p. 600.



Vole-like forms with blunt faces. Chunky build, often shaggy, grizzled or striped. Herbivorous.

Laminated teeth, p. 562.
non-laminated teeth.
M1 with 3 cusps in first toothrow, p. 605.



Short-legged forms, small dumpy build. Small to medium size (H. & B. 50—190 mm). Specialized species.

M1 with 2 cusps in first toothrow, p. 555.
Grooved incisors, fat, p. 543.
M1 with 3 cusps in first toothrow.
Spiny fur, p. 654.
Brush-like fur, light coloured, p. 652.
Brush-like fur, dark coloured, p. 646.

RAT-LIKE (MUROID) RODENTS

Very long pointed face, sandy-coloured back, white below, p. 536.
 Rounded muzzle, dark above, white below, p. 662.
 Rat-like face, brown above, grey below, p. 667.

Long-limbed quadrupedal forms. Forest habitats.



Large eyes, laminated teeth, drier habitats, p. 507.
 Pygmy size, high altitude swamps, p. 558.

Long-legged jumping forms.



Medium size (H. & B. 100—150 mm).
 M1 with 3 cusps in first toothrow, p. 630.
 Small size (H. & B. 50—100 mm.).
 M1 with 2 cusps in first toothrow, "hooked" hand, p. 528.

Arboreal forms with long tails.



All habitats, p. 672.

Dormice—bushy-tailed.



Mountain and rocky country in forest or thicket, p. 519.

Maned rat, long-haired with strong black, white and grey pattern.



Cricetid Rodents

Cricetidae

The cricetids are clearly a very old group, this is betrayed by their great diversity and by their huge range, which includes the Americas where, without competition from the murids, they have radiated into all the rat niches. Significantly, they are absent from the tropical zone of Asia, the main home of the Muridae.

In Africa, where Muridae are more recent arrivals, Cricetidae are present either as relics or as specialists. Three genera with rat or mouse-like forms certainly seem to be in decline, these are *Beamys*, *Delanymys* and *Deomys*; for the last of these species there is good evidence that this declining status is the result of competition (see p. 542).

In Africa, many of the cricetids are slower, more sluggish animals than the murids and this limitation must affect these species in several ways; they must have smaller ranges, which would reduce social and sexual contacts and during difficult periods reduce food availability; they must be more vulnerable to predators and they may also be less capable of standing up to more aggressive and active competitors. In addition to these disadvantages they appear to be less prolific and grow more slowly.

The living cricetids have offset these limitations by various means. The gerbils have sharp eyesight, can run fast and dig holes, all qualities that serve them well in dry, open habitats where few murids can compete with them. The most bizarre species is the maned rat, *Lophiomys*, which exhibits the behaviour of an aposomatic. The exceptional size of *Cricetomys*, the giant rat, places this animal in a class of its own but, like all the pouched rats, it has specialized in food-gathering by means of its pouches and also 'camping' near a rich food supply. The Cricetomyinae were first put into the Cricetidae by Petter (1964) and the Dendromurinae were also assigned to this family very recently (Lavocat, 1959). The Dendromurinae are mostly very small climbing mice that have specialized in grass-seed eating, a niche where their main competitors are more likely to be birds than other rodents. The Otomyinae have become more truly herbivorous than any other rat and their broad incisors and laminated teeth are well adapted to graze on grass stems. Their sluggish, mild temperament and small litters do not stop them from being a dominant species in some of the moister grassland types, but their interaction with advanced, herbivorous murids, like *Arvicanthis*, is discussed in the profiles. The rare *Delanymys* seems to be hovering on the verge of extinction in its mountain refuge.

The patterns of the molar teeth are some measure of the family's diversity.

There is some evidence from captives that Cricetids may live longer than most Murid species.

Gerbils

Gerbillinae

The name gerbil derives from an Arabic word that alludes to their well-muscled hindlegs, a character that immediately helps to distinguish them. These powerful long-footed hindlimbs contrast with short, clawed forelegs: the former enable the gerbils to make great leaps, while the latter allow them to dig proficiently. Other characteristics are relatively large eyes and very inflated ear bullae on the skull.



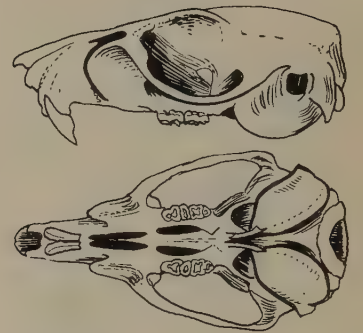
Skeleton, *Gerbillus harwoodi*.

Gerbils range through the drier areas of Africa and Asia, and some forms live in very arid desert conditions and countries. Their tunnelling habit is undoubtedly a most important factor in the success of the group; this rapidly made shelter provides a refuge from a hostile environment and from the increased danger of predators that exists in an exposed habitat. For some species it allows food to be stored and for all of them it provides a place in which to hide and have young. These are born naked and blind and develop relatively slowly, only opening their eyes during the second or third week of life. Their principal foods are seeds and vegetable matter, but they are probably fairly opportunistic feeders.

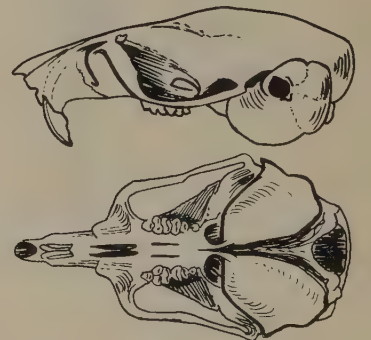
A comparative study, mostly of North African forms, has been made by Petter (1959).



Tatera (boehmi).



Taterillus (emini).

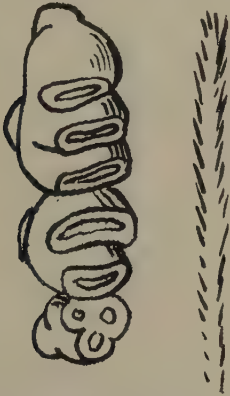


Gerbillus (gerbillus).

KEY TO THE SPECIES OF TATERA

Afra group

Dull colouring, short-haired tail,
broad molars, bright-coloured
feet



Tatera valida

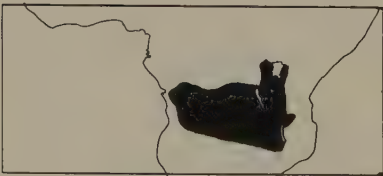
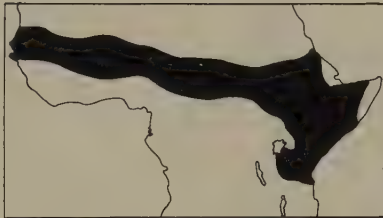
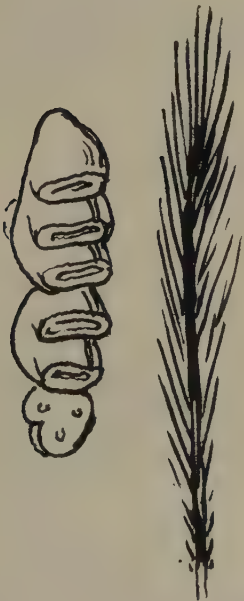
H. & B. 112—190 mm
T. 120—180 mm
Hf. 27—37 mm
Ear 22—24 mm

Tatera inclusa

Tail occasionally white tipped
H. & B. 145—175 mm
T. 152—185 mm
Hf. 37—39 mm

Robusta group

Long-haired, dark tail tip.
Narrow molars, thin
dark-coloured feet



Tatera robusta

Tail not entirely black
H. & B. 110—160 mm
T. 139—190 mm
Hf. 32—35 mm

Tatera nigricauda

Tail all black
H. & B. 120—160 mm
T. 160—204 mm
Hf. 35—38 mm

Tatera leucogaster

Divergent outer tubercles on laminae
H. & B. 120—136 mm
T. 130—176 mm
Hf. 29—35.5 mm

White tassel tip to tail



Tatera boehmi

H. & B. 155—185 mm
T. 210—245 mm
Hf. 43—44 mm

Tatera Gerbils (Tatera)

Tatera Gerbils (Tatera)

Family Cricetidae
Order Rodentia

Tatera includes some very widely distributed species and the genus is found over most of the non-forested areas of Africa and also in Arabia, Persia, India and Ceylon. Eight species are known from this continent, six of which are represented in East Africa.

The habitat may vary somewhat from species to species but most of them prefer sandy soils and relatively open, well-drained areas in which to dig their fairly elaborate burrows, which are about 50 cm deep. A pair dig a burrow system that can extend over as much as 10 sq. m and generally includes one or more enlarged chambers and also a grass-lined nest. Their burrows are probably an important factor determining their success *vis-à-vis* other rodents. Where there is limited natural shelter from sun, fire, and predators in dry open habitats, the *Tatera* gerbils escape the rigours of temperature fluctuations and desiccation by staying in their burrows by day and they also gain some advantage in the dry season when fires burn off most of the cover. It is where such conditions prevail that these gerbils flourish.

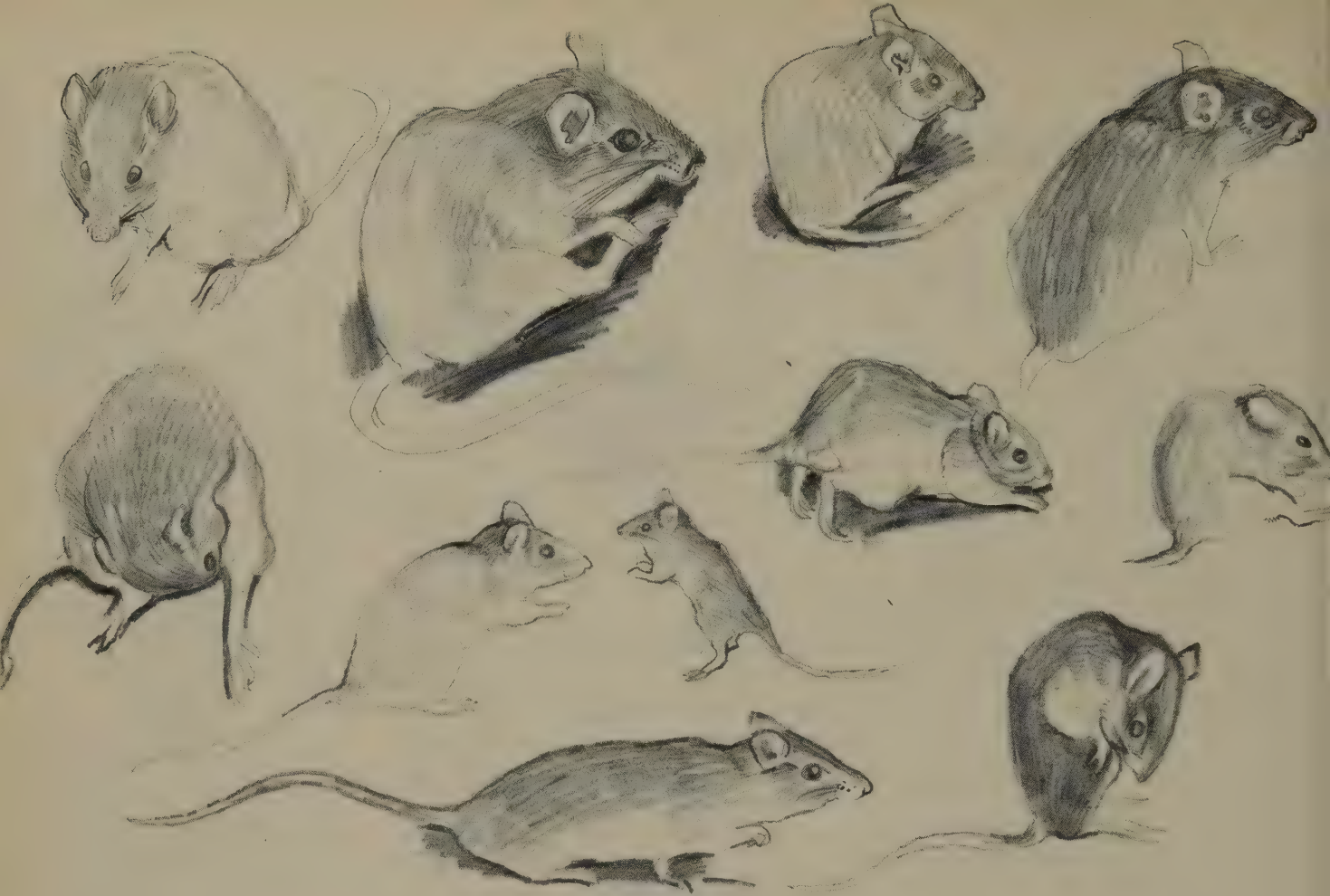
They seem to be opportunistic feeders, living off the roots' dry bases and the stems of burnt grass during the dry season, but taking grasshoppers, termites and other insects when these are plentiful. Grass seeds, other grains and fruit are eaten when available and also fresh grass. Roots and bulbs are dug out and crops such as cassava and groundnuts are sometimes damaged in cultivated areas. When food is scarce, they probably range over many hundreds of metres each night foraging. They are apparently able to go without water for long periods; liquid has, nonetheless, been found in some quantity in the gut.

A pair or family live in one home burrow for months at a time but may desert a burrow or locality for another from time to time; what controls this movement is not known. Very little is known of the details of their social life; some species appear to be more gregarious than others. Also fluctuations in the density and numbers of populations have been noticed.

Knowledge of their biology is important as they have been found to be carriers of bubonic plague in South Africa and fleas flourish in the nests of some species in some areas. However, they are not found near buildings and their role in plague transmission is principally that of providing a reservoir of infection. They are regarded as a delicacy in some areas and are dug out of their burrows and taken home as food. Where this practice is common the potential for infecting house rats exists.

Other predators are mostly nocturnal carnivora, owls and snakes but I have seen *Herpestes (Myonax)* systematically exploring a *Tatera* burrow by day.

Gestation is about three weeks and the 4 to 8 young are born like other gerbils in an undeveloped state and must remain in the nest for a month before accompanying the adults out to forage.



T. v. valida.

Tatera valida is the commonest and most widespread species. It is also the most rat-like in appearance. There are several well-marked geographic races, two of which range over most of East Africa, *T. v. nigrita* in Uganda and southwestern Kenya and *T. v. taborae* in Tanzania. A population in the vicinity of Mombasa has been described by Davis (1968a) as an isolated relic group of white-bellied short-tailed gerbils which are obviously distinct from *T. v. taborae* and have, instead, affinities with *T. v. valida* of Angola and the southeastern Congo.

Vesey-FitzGerald (in preparation) has drawn attention to an interesting situation on the Ufipa Plateau, a highland zone between Lake Tanganyika and Lake Malawi which separates the distinct races, *T. v. taborae* and *T. v. valida*. This area has been settled by humans in recent years. The original forest and woodland has been cleared and the open fallow land that forms after cultivation would seem to have been invaded by gerbils from both east and west.

T. v. taborae is distinguished by the possession of deeply grooved upper incisors and one pectoral and two inguinal pairs of mammae (i.e. $1 - 2 = 6$); *T. v. valida* on the other hand has faintly grooved or smooth incisors and a mammary formula of $2 - 2 = 8$. Vesey-FitzGerald found that 40% of the Ufipa gerbils had the latter mammary formula and 60% the former, while 84% had markedly grooved upper incisors, 8% were smooth and 8% were shallow. The most detailed account of their habits is that of Vesey-FitzGerald (1966):

"This gerbil inhabits well drained sandy soils, above flood level, on the perimeter of valley grasslands. It is particularly abundant along the edges of flood plain grasslands in the Rukwa valley where its honey-combed warrens may extend for many miles along a belt facing the tree line. It is also common in sandy alluvium along rivers, and in old gardens where the soil has been loosened by cultivation. It feeds on the underground parts of grasses and sedges. In compact soil these roots are obtained by shallow excavations, but in loose soil superficial tunnels are made and the rhizomes are gnawed from below the surface. This activity very soon destroys all the herbaceous vegetation and the surface of *Tatera* warrens is therefore characteristically bare and honey-combed, especially during the dry season. During the rains when the grass is long and there is less nutrient stored in their parts underground, the gerbils feed on green grass blades. These gerbils are extremely sedentary and seldom leave the vicinity of their holes. Typically the burrow has one or more open entrances giving access to tunnels which descend gently to a chamber 18 in to 2 ft (45—60 cm) below the surface. From the chamber there is usually a steeply ascending escape passage which just reaches the surface but is not opened except in an emergency. The larger warrens consist of a collection of such groups of holes, each entrance leading to a chamber, but they are not usually interconnected, and the inmate defends its shelter from intruders. Well marked surface runs lead from one entrance to another, and these may traverse short distances of open country to adjacent warrens. . . . Predators are avoided by remaining in the close vicinity of their protective holes, but the serval cat, *Felis serval*, and the wild cat, *Felis libyca*, are regular nocturnal visitors to gerbil warrens, where they lie in wait near the holes and pounce on the rats as they emerge. Snakes find shelter within the warrens themselves, and the puff-adder, *Bitis arietans*, is an important predator of the adults and the house-snake, *Boaedon fuliginosus*, of nestlings".

This species is also common in fallow land near cultivation and is very numerous in some localities and may be subject to fluctuations in population. Hopkins notes that there used to be very many old deserted warrens on the Entebbe peninsula which were thought to be evidence of an epidemic attacking the gerbils at some time in the past. Hopkins remarks

"the rarity with which fleas are obtained on the species in most areas makes it very improbable that the infection in question was plague, although a specimen captured in Kampala has been recorded as plague infected. It practically never enters human habitations".

The British Museum expedition to the Ruwenzoris reported

"these rats are very numerous on the plains around the south end of Ruwenzori, but were almost impossible to catch. We failed to locate them in any holes and they appeared to feed only upon young grass stems, of which they cut up great quantities into short length of from 2—4 inches long, but they refused all baits".

The maximum number of young seems to be 6, the minimum is 2. A detailed diagram of the burrow of this species is published in Verheyen and Verschuren (1966).

T. inclusa is distributed east of Lake Malawi in the "Mozambique zone". An almost black form, *T. i. pringlei*, has been described recently from Muheza, Tanzania (Hubbard, 1970b), which may be a distinct species.

Tatera robusta with its well-marked black tuft on the tail is a common gerbil of the northern savannas and inhabits the drier parts of Kenya and northern Tanzania.



Tatera leucogaster is a southern woodland species found from South-west Africa to southwestern Tanzania. Vesey-FitzGerald describes this species as occurring in sandy soils

“The bush-gerbil, *Tatera leucogaster* occupies sandy soils of woodland and riverine herbage, where it excavates burrows leading to a chamber 20—45 cm below the surface. The chamber is often lined with dry grass. There are usually one or two other tunnels forming escape routes but the hole groups of this species are normally small and scattered. Surface runs under the ground herbage are usually well marked and *leucogaster* feeds at some distance from its holes”.

Powell (in Shortridge, 1934) describes these animals in South Africa

“there may be thirty families in an area of land a mile square, but one would find perhaps 130 warrens. In a week or ten days one warren may have been occupied by three or four families at intervals; this state of affairs extends from one end to the other of the sand-veld. In the winter or during any scarcity of little bulbs and sweet grass roots which are their main food they are apt to migrate to low-lying ground. In the rainy season they will migrate to higher ground so as to avoid floods. They seem to become very numerous around the edges of cultivated lands, and these are sometimes so badly riddled with burrows as to spoil the crops”.

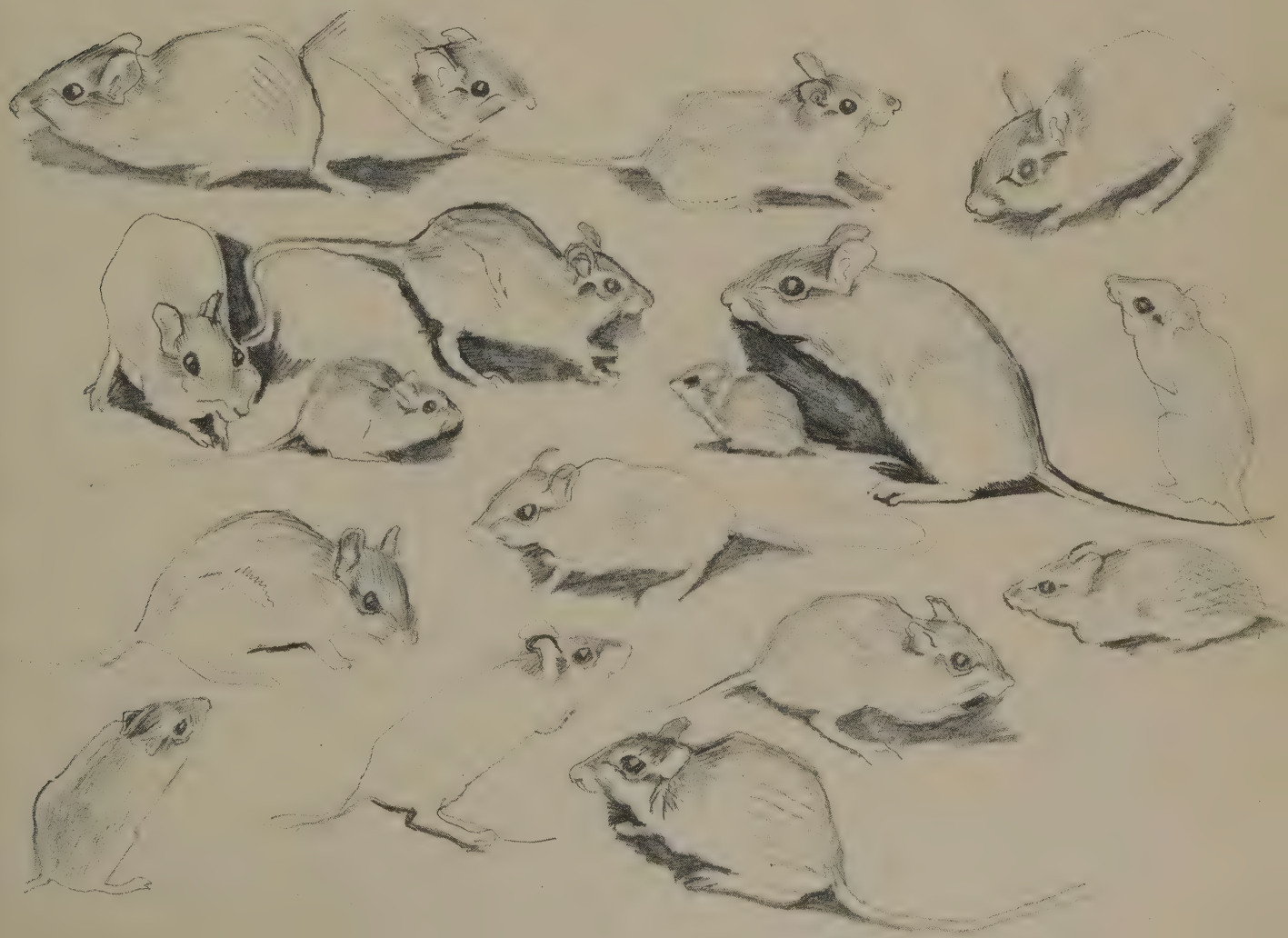
Tatera nigricauda is a northeastern African species, ranging from southwestern Ethiopia to northern Tanzania and eastern Uganda. Its habits resemble those of the other *Tatera* species.

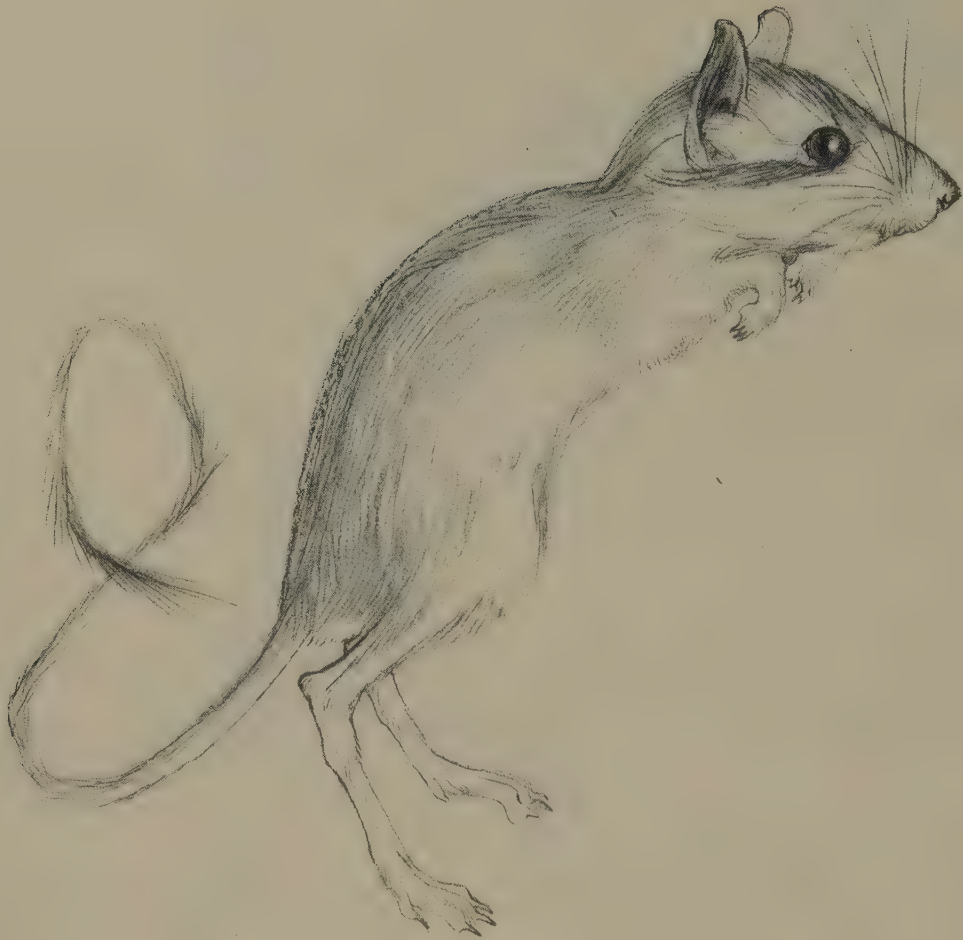
Tatera (*Gerbilliscus*) *boehmi* is a brightly coloured, long-footed gerbil restricted to the southern savannas. Roosevelt (1910) describes them living on open plains among grass. Each animal having several burrows with little mounds at the entrance. I have found them living in open woodland in southwestern Tanzania, particularly in old millet fields where shifting cultivation has been practiced. In the Rukwa area Vesey-FitzGerald reports this species thicket vegetation

“it also associates with both *liodon* and *taborae*. Its burrows have only one or two entrances which are not marked by much excavated soil. Frequently the burrows of other species of *Tatera*, or the long tunnels of mole-rats, *Cryptomys*, are used. This species is strictly nocturnal, and its forays extend over wide areas”.

◀ *T. leucogaster*.

T. leucogaster.





Taterillus Gerbil
(Taterillus emini)

Family Cricetidae
Order Rodentia

Measurements
head and body

100—144 mm

tail

130—190 mm

hindfoot

28—35 mm

Taterillus Gerbil (*Taterillus emini*)

Taterillus is principally distinguished as a genus by the very large cavities of the palatal foramina. In most other respects it appears to be a small type of *Tatera*. There is probably only one species which is regionally variable; it is sandy buff to dark brown on the back, with white belly, hands and feet. A dark mark runs behind the eye to the base of the ear. The eyes are particularly large and the ear bullae somewhat smaller than in most other gerbils, suggesting a slightly different behaviour pattern for this gerbil. As this type of gerbil is not found in true desert, an extreme development of the bullae may be less important than in some of its desert-dwelling relatives. It ranges over the Sudanic savannas and steppes south of the Sahara from Senegal to Ethiopia and Kenya, and it lives on open, dry and well-drained soils on plains, in savanna woodland or in thorn scrub. It has adapted to the secondary vegetation around villages and to cultivation.

Its burrow resembles those of *Tatera* species, being about 50 cm deep and situated on bare, well-drained soils. Excavated earth is not piled up around the several entrances, which are kept closed with sand from within by the occupants.

They feed on a variety of vegetable matter and some have been caught with meat baits (Rosevear, 1969). Verheyen and Verschuren (1966) noticed the remains of *Solanum* in a burrow, which suggests that food may be carried home to be eaten.

The animal is strictly nocturnal; if excavated in daylight it rushes for the nearest burrow and immediately blocks itself in with earth. Watson (1950) describes their "escape hatches, which terminate just below the surface of the ground".

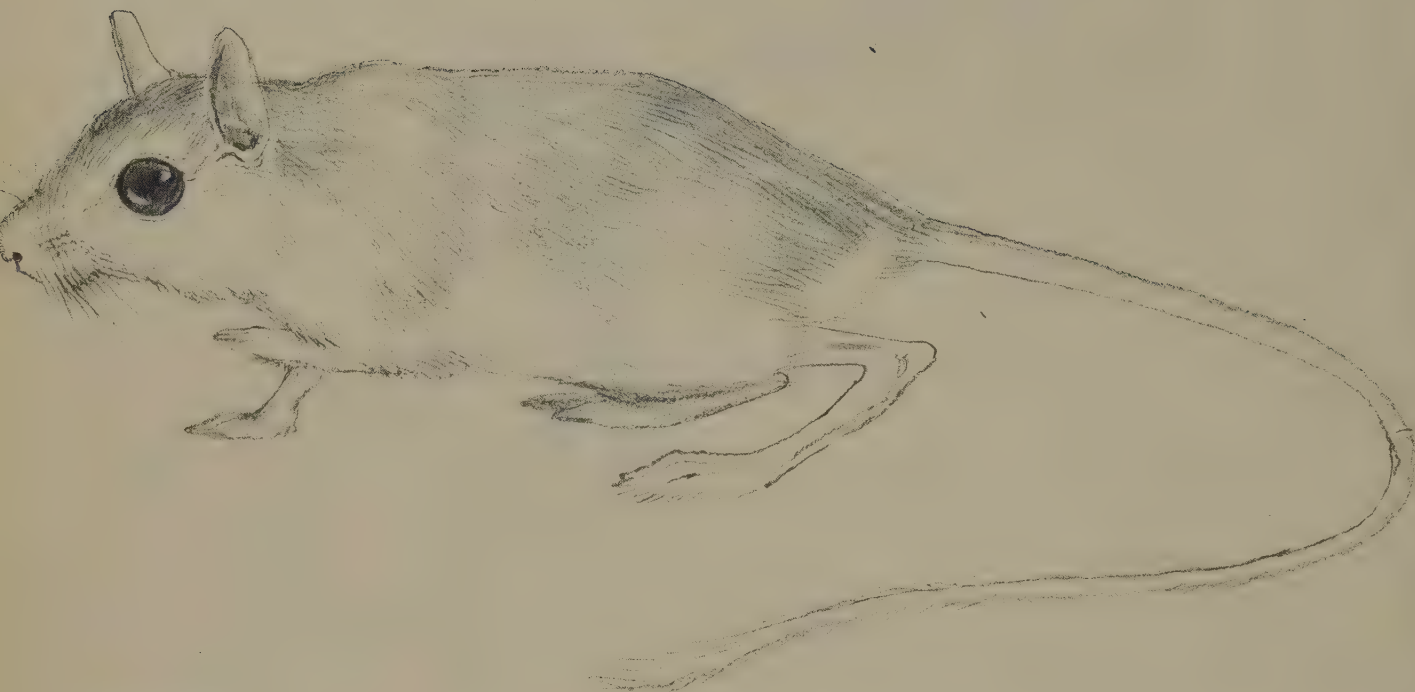
"When danger threatens from below the Gerbil flees up this bolt hole, bursts through the thin crust of earth at the top with, according to a Karamojong informant, sufficient force to propel itself well into the air, and then scuttles away to the safety of another warren. The Karamojong are well aware of this habit and the vernacular name 'lonong' is derived from the word 'anang', meaning to punch out, there being apparently some similarity between this action and the sudden 'jack-in-the-box' appearance of the Gerbil above ground".

In comparison with desert gerbils *Taterillus* may have different habits because of the relatively richer vegetation providing a less dispersed food supply and more cover. It might be possible to correlate the less swollen bullae and the very large eyes with such environmental considerations when more is known about the animal. Information on total range, modes of communication and the relative importance of the senses for various types of gerbil would therefore be interesting.

Taterillus forms small colonies but populations are subject to fluctuations, which must regularly alter their social structure and ecology. Verheyen and Verschuren report a widespread increase in numbers in the Garamba National Park in the northeastern Congo in July 1952.

Very little is known of their breeding behaviour but it probably resembles that of *Tatera* with the young born in the burrow in a very underdeveloped condition.





Gerbillus gerbillus.

Egyptian Gerbils (Gerbillus)

Family Cricetidae
Order Rodentia
Local names

Mbadya (Kigogo), Mogullu
(Kitaita and Kisagalla)

Measurements head and body

80—100 mm

Gerbillus gerbillus

tail 102—130 mm

hindfoot 22—26 mm

head and body

75—86 mm

Gerbillus harwoodi

tail 96—112 mm

hindfoot 21—22 mm

head and body

85—98 mm

Gerbillus pusillus

tail 100—110 mm

Egyptian Gerbils (*Gerbillus*)

Species

Gerbillus gerbillus

Gerbillus harwoodi

Gerbillus pusillus

Gerbillus is a genus of small gerbils found in the drier parts of East Africa and represented by four forms. They are distinguished by their long hind legs and short front legs. Their skulls possess swollen ear bullae and enlarged mastoids. One species *G. gerbillus* has hairy soles to the hindfeet, the others have naked soles.

The genus is distributed over all the drier parts of Africa and Arabia, Iran and northern India. At present too little is known of the individual species to describe specific habits, although there is evidently some ecological differentiation between species dwelling in different geographic and climatic areas.



They are sometimes to be seen running or hopping about on murram roads at night, and they seem to prefer open sandy soils; most species appear to like alluvial areas that are flooded in the wet season and dry out in the long hot season. Some species shelter in the deep ground cracks formed in such soils and all species seem to make less elaborate warrens than other gerbil genera. Their homes often consist of little more than an excavated sleeping chamber. This simple shelter may reflect a more nomadic mode of existence and seasonal movements, or may be determined by the physical exigencies and edaphic conditions of their chosen habitats. There are certainly seasonal changes in burrow sites. Loring (in Roosevelt, 1910) describes differences in burrow formation for *Gerbillus harwoodi*:

"On the sandy desert flats on the southwest side of Lake Naivasha they were abundant. The holes running obliquely into the ground were sometimes blocked with sand from the inside. On the opposite side of the lake there was less sand and here the gerbilles were found only in spots. In the sand alone the burrows resembled those described, but where the ground was hard they entered almost perpendicular and were never blocked. Often seed pods and tiny cockle burrs were strewn about the entrances".

They are sometimes gregarious, making groups of burrows in choice spots, but details of the social composition of these colonies are not known. Petter (1961) found well-worn paths leading from the burrow to feeding areas which were evidently used frequently.

They feed mainly on grass seeds, grass stems and roots, but also fallen fruits, nuts and some insects. Carrion is said to be taken by some species on occasions. Some types are known to forage many hundreds of metres from their shelter and have been reported to be attracted towards grass fires, presumably by grasshoppers and other insects fleeing the conflagration.

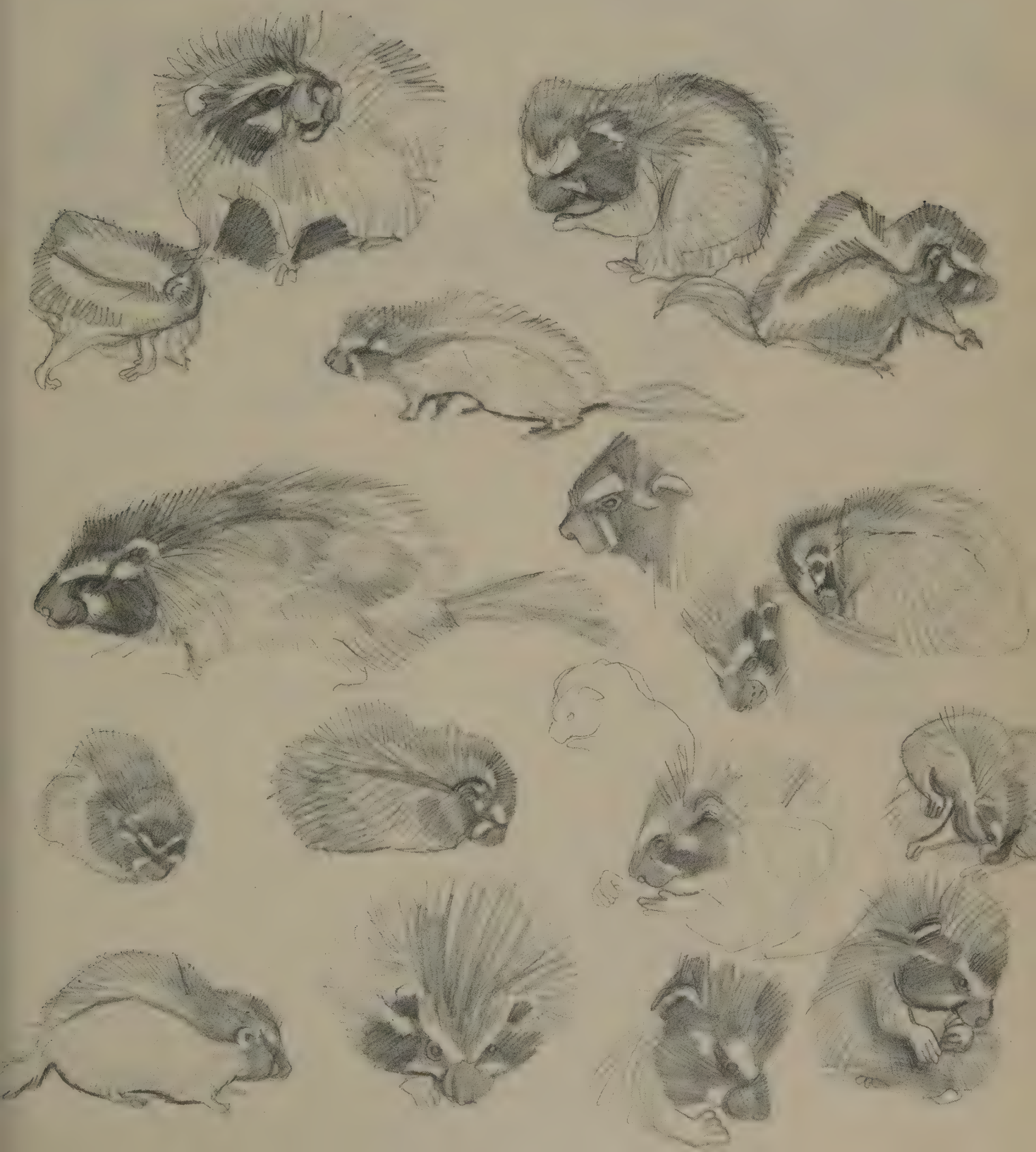
Like other gerbils they are entirely nocturnal. They are probably hunted by a variety of small carnivores, owls and snakes. One has been recovered from a sandboa, *Eryx*, at Voi.

They are probably seasonal breeders and Loveridge (1937) found half the South Kenyan series of *G. pusillus* were immature in April, suggesting a birth season or peak for this species in about February or March. Gestation is in the region of three weeks and the nest in which the young are born is lined with the hair of the mother's belly. The new-born gerbil is blind and naked, with closed ears which unfold in about a week, when hair begins to grow. The eyes open and the teeth break through at about two or three weeks of age. Captive *Gerbillus* have been kept up to 6½ years of age.

Crested Rats

Lophiomyinae

This subfamily contains the single species *Lophiomys imhausi* which is described in the following profile.





Crested Rat
(*Lophiomys imhausi*)

Family Cricetidae
Order Rodentia

Measurements
head and body

255—360 mm

tail

140—215 mm

weight

590—920 g

Crested Rat (*Lophiomys imhausi*)

This extraordinary rodent has been the source of a great deal of speculation. Its appearance has been compared with that of many other animals. Hollister thought the animal suggestive of the Canada porcupine, *Erethizon dorsatus*. Others have thought it resembled a zorilla, *Zorilla*, or an opossum, *Didelphis*, or a moon-rat, *Echinosorex*. The unique skull is roofed over with bone so that the form of the cranium resembles nothing so much as a turtle.

These comparisons appear to have little in common but are in fact not as far-fetched as they might at first appear. The Canada porcupine is a slow arboreal rodent protected by its quills and its threatening display; the vulnerable Virginian opossum shams death as a defence, while the insectivore, *Echinosorex*, emits a very distasteful smell like the carnivore *Zorilla*. Were it not for their various protective devices, each of these animals would be very vulnerable, for neither their black and white colouring nor their behaviour patterns are conducive to escape from enemies. Furthermore, when harassed, these animals merely erect fur or crests, which make them even more conspicuous and create the illusion of greater size. These are essentially superficial characteristics which this odd assortment of animals share with *Lophiomys*, giving each a certain visual similarity.

It has been suggested that *Lophiomys* is a harmless mimic of the zorilla or perhaps of the African porcupine. However most mimics are very close imitations of their model, and *Lophiomys* is a very poor copy of both these animals. A great deal remains to be learnt about *Lophiomys* but there is some evidence to suggest that this rodent possesses toxic properties. These might take the form of pathogens in the saliva, or they might be connected with the peculiar tract of differentiated hairs running down the animal's sides. These hairs have normal tips but are thick and fibrous for most of their length and resemble jute string when seen under a microscope. They are absorbent and generally appear to serve as spongy receptacles for a slightly greasy secretion originating from the glandular area in which these hairs grow.

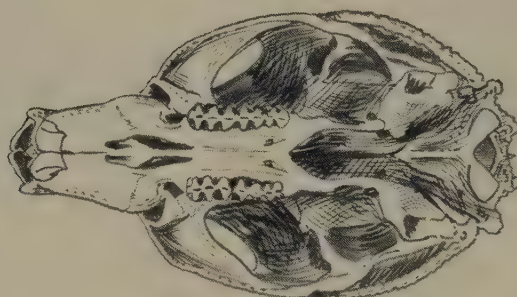
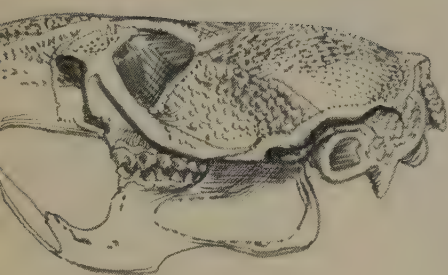
Most of the body is clothed in long, black and silver-tipped guard hairs growing out of a dense woolly grey and white undercoat, only the face and feet having short blackish fur. The side glands are normally completely hidden in this fur until the animal is excited, whereupon the hair parts, exposing the brown glandular strip. Above and below this, the folding back of the fur creates bold white and black stripes that draw special attention to the exposed gland. When the animal is bullied, it throws its body from one side to the other, presenting its very conspicuous flank to its attacker, meanwhile hissing, snorting, growling and snapping with the teeth if approached closely.

A reliable informant in Kenya has described dogs dying after attacking *Lophiomys*. The dogs initially foamed at the mouth, a typical reaction to certain irritant poisons. The Wanderobo huntsmen, who know *Lophiomys* well, will not handle it for fear of its bite which they say is poisonous. Unfortunately, the saliva and glandular secretion of *Lophiomys* have not been tested for toxins or pathogens, but a thorough study of this, and other aspects of *Lophiomys* biology, should be interesting.





Lophiomys is long-backed and short-limbed. It has very broad mobile palms with well marked pads on the forelimbs and very broad hindfeet. The role of the coat in enlarging the animal's size is illustrated in the drawing opposite. The peculiar roofing over the cranium is due to an extension of the orbital margins of the frontal and the squamosal, thus entirely surrounding the eye with bone and presumably giving it added protection. The parietal has also extended, linking with the frontal and squamosal to cover completely the temporal fossa. This arrangement is reminiscent of a false hull on a boat and indeed its function may be to take the impact of attacks so that the chance of damage to the eyes and brain are reduced. The roofing bone is very granulated and this texture is characteristic of all the bony areas on the top of the skull and seems to be associated with a general reinforcement of the exposed areas of the head.



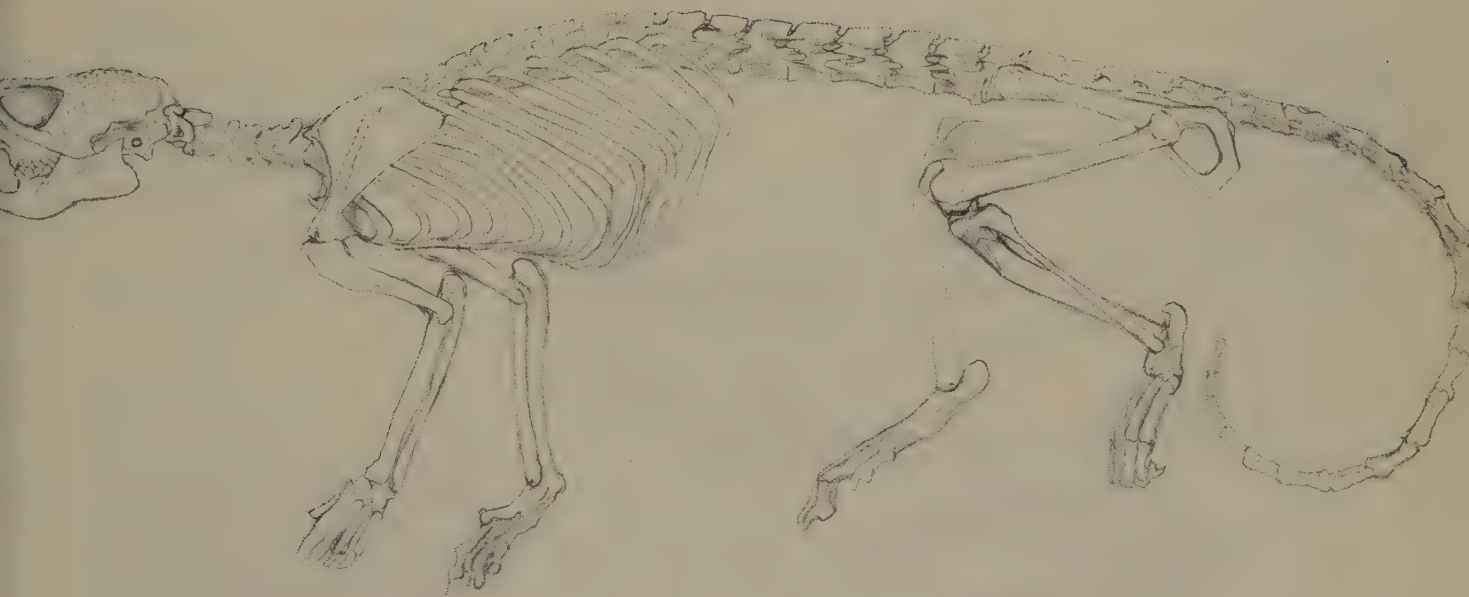
The animal is only known today from parts of Somalia, Ethiopia, Sudan, Kenya, Uganda and Tanzania, but its range must have been very much more extensive in the past as a sub-fossil has been discovered in Israel (Dor, 1966).

The commonest habitat is forest or woodland on the drier mountain massifs or highlands; over most of East Africa it occurs between 1,200 and 2,700 m although it might live at lower altitudes in parts of Somalia. It is often found in rocky areas and lies up in hollow dead trunks or in holes that are frequently situated on the edge of ravines or in bushy banks. Heller snared *Lophiomys* in a hyrax runway among rocks on a cliff.

"These three specimens were caught in rock crevices above permanent water in an old creek bed in rank, weedy vegetation. The two females were quite gentle and could be stroked after being taken from the traps. They were slow and dazed in their movements, but when disturbed made a series of faint puffs or sneezes, apparently to alarm the aggressor. The old male, however, bit savagely when irritated and made a coughy, sneezy bark when angry. Held by the tail, they were unable to turn up and bite".



The diet in the wild seems to include leaves, fruit and shoots, but in captivity they accept various root vegetables and cereals and will eat meat or grasshoppers. They are fond of sweet potato leaves and have been reported to favour salad endives. Bananas have been used as an effective bait for traps. *Lophiomys* does not have to drink regularly; presumably its food provides adequate moisture. Its feeding is slow and deliberate and food tends to be eaten where it is found. The animal squats and uses its forepaws to manipulate the food and lift it to the mouth. The very small "thumb" is divergent







from the other digits and enhances the animal's skill in handling things. As the animal tends to be quite indifferent to its surroundings, the lack of any visible reactions does not admit of an assessment of its sensitivity to smells, sounds or sight. The animal figured here was found walking on a path near Moroto. A passer-by with a four-gallon petrol tin placed this in front of the *Lophiomys*, whereupon it just walked into it.

Ellerman's experience (Ellerman 1940) of keeping these animals is typical:

"Some time ago I was fortunate enough to obtain some of these interesting animals, some of which I gave to the London Zoological Gardens, and some of which were kept by a friend of mine. They lived quite well for a time, and moreover, my friend bred and reared a single young one which lived for 14 months. The diet was the chief difficulty in keeping these animals alive, and the problem was not solved. They seemed to thrive best in a temperature of about 60 degrees. They were rather strictly nocturnal and at first not easy to tame; but when placed in a large cage and given a hollow log to sleep in and plenty of climbing facilities, they soon got to know us and would come to call and feed from the hand in the evening. I have seen it stated that these animals cannot climb; my impression is that they are the most perfect and natural climbers.

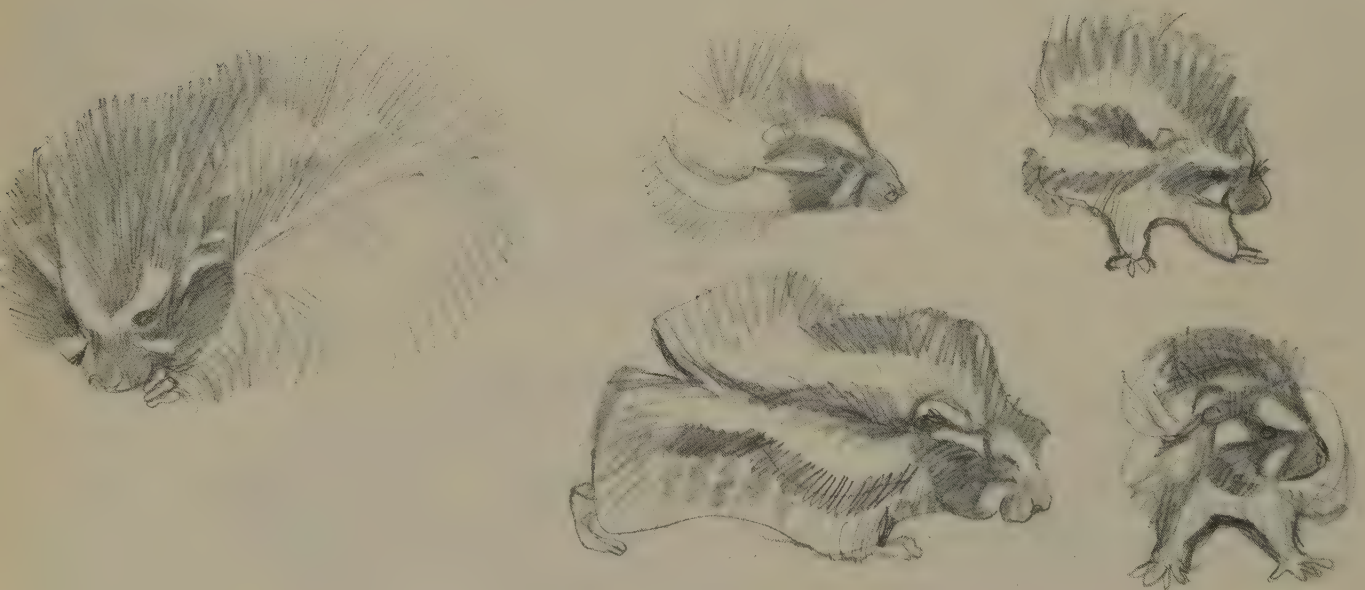
When provided with a cage about six feet high they lost no time in climbing to the top of it, and they always climb down vertical wire netting head downwards and front feet first; even the young one which was bred doing this rather astonishing feat quite naturally; moreover they seemed able to swarm up concrete for a short distance. On the whole they were very slow moving animals, and it is rather a mystery how they have managed to survive''.

Although they are generally nocturnal, the Moroto animal was abroad in daylight. They are usually seen singly but pairs have been found together and also females with young. Obviously scarce animals all over their range, they seem to be slightly more abundant in some localities, notably the juniper forests around Mt Kenya.

It is not known how large an area an individual ranges over, nor how attached it is to the home burrow. It is impossible at present to guess what factors limit this species to its present range. Its rarity and perhaps its nocturnal habits have tended to hide its presence from the lethal human predator and there are no data on other enemies. Its range of ecological habitats is reasonably catholic and it co-exists with hyrax and other rodents which could be regarded as competitors.

Plague fleas have been found in the coats of *Lophiomys*, also the rare *Amphopsylla conversa* whose other principal known host is an entomologist (see McRae, 1965).

Nothing is known of their breeding behaviour, except that two or three young are born at a time. The young are well haired at birth and grow rapidly. They are apparently quite fearless.



Dendromurines

DENDROMURINAE

Dendromús
Steatomys
Deomys

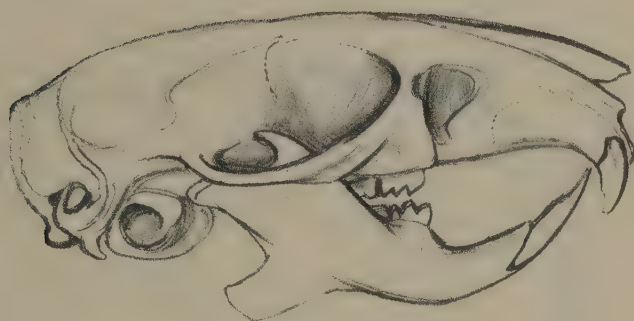
This exclusively African group of rodents contains three highly specialized genera. The group has been placed in the Muridae in the past, but after comparing fossil forms with the living *Dendromus* and *Steatomys*, Lavocat (1959) showed that the group was almost certainly cricetid, a classification that has been generally accepted since.

It seems that before the arrival of the true murids from tropical Asia, African cricetid rodents had gone a long way towards filling the many rat and mouse niches. The biserial pattern of the cricetid teeth was elaborated by extra cusps in some forms, notably the Dendromurinae and Cricetomyinae, perhaps in order to achieve a broader grinding surface and better occlusion. This addition gives the teeth a similarity to the typically murid triserial teeth.

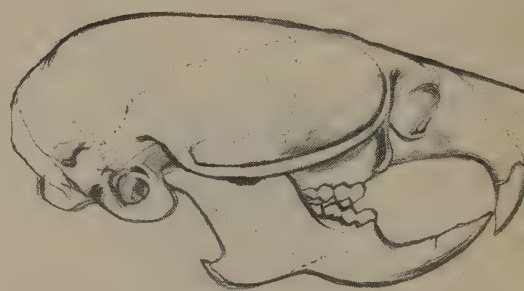
With the arrival of the murids there was probably a general decline of all cricetid groups. The living Dendromurinae seem to have escaped competition by being sufficiently specialized not to enter into competition with any murid group. The exception is *Deomys* which is discussed in the profile of that species.



Steatomys pratensis tooththrow.

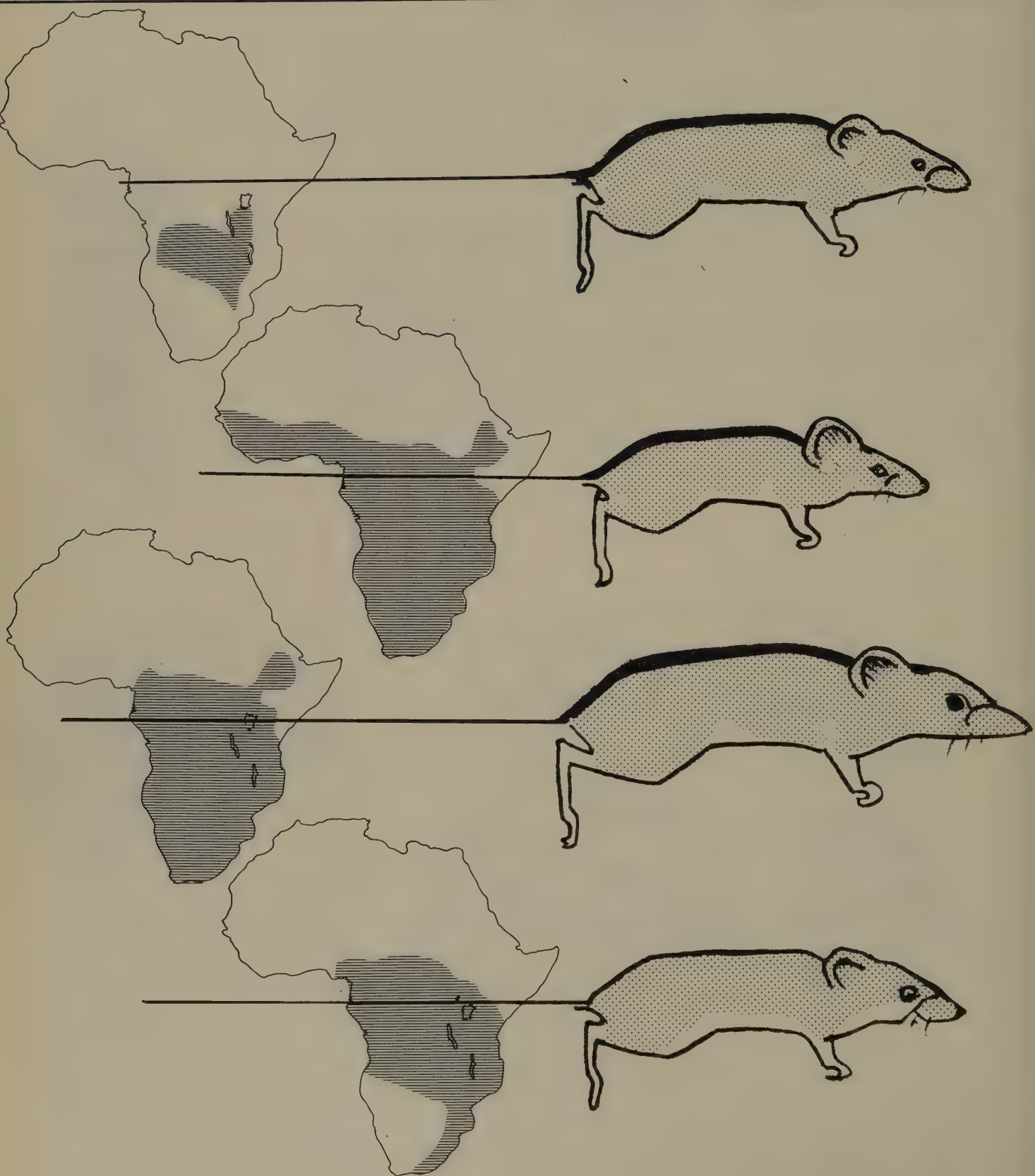


Steatomys pratensis.



Dendromus melanotis.

KEY TO



DENDROMUS SPECIES

Species

Measurements

Dendromus nyikae

H. & B. 75 (72—81) mm
T. 86 (77—93) mm
Hf. 18 (17—19) mm
Ear 15 (11—16.5) mm
Skull 21—23.1 mm
Wt. 12—18 g

Dendromus melanotis

H. & B. 65 (57—73) mm
T. 75 (65—80) mm
Hf. 18 (16—19) mm
Ear 15 (11—16) mm
Skull 19—21 mm
Wt. 7—8 g

Dendromus mesomelas

H. & B. 69—100 mm
T. 85—113 mm
Hf. 18—22 mm
Ear 11—15 mm
Skull 22—25 mm
Wt. 11—21 g

Dendromus mystacalis

H. & B. 70 (50—80) mm
T. 83 (72—101) mm
Hf. 17 (14—20) mm
Ear 12 (10—14) mm
Skull 16—22 mm
Wt. 7—17 g



D. mystacalis.

**Dendromus Mice,
Climbing Mice
(Dendromus)**

Family

Cricetidae

Order

Rodentia

Local names

Nandalanendu (Kikinga),
Cheptoragopsi (Masai),
Chapchorogos (Sebei), Mandiosi
(Gisu), Mulubendi (Lubukusu),
Isorodoni (Tereki), Daa (Kisambaa),
Kamampi, Kumi (Kuamba),
Kangoma, Kuinji (Lukonjo),
Mbebawairungu (Lutoro),
Siyebo (Kinyika)

Dendromus Mice, Climbing Mice (Dendromus)

Dendromus is divisible into two types, each of which has a larger and a smaller species. The pictorial key illustrates the characteristics of each species.

As their name implies, climbing mice are specially adapted to climb on thin stems and to this end all types are small and light. Their limbs have been modified to grip very thin vertical supports and their prehensile tail is used for additional support.

They are widely distributed south of the Sahara but do not occur in true forest nor in the most arid areas. The species have differentiated to fill distinct ecological zones and although they are sympatric in some localities, for the most part they exploit the grass-seed eating niche independently. Dieterlen (1971) has pointed out that whenever *melanotis* and *mystacalis* are put together they fight ferociously, a fact which presupposes competition in

Species

Dendromus nyikae

Dendromus melanotis

Dendromus mesomelas

Dendromus mystacalis



the wild. Where these two species are sympatric there is probably a fairly clear division in their micro-habitats but frequent contacts cannot be excluded. The precise niche of a particular *Dendromus* population is probably modified and defined as much by competition with other *Dendromus* species as it is by the climate and vegetation.

That this may be so is suggested by the figures presented below from two localities from eastern Zaire (Congo). The first table shows Misonne's results in Haut Ituri (1963) where *D. melanotis* is absent, the second shows the relative numbers caught by Dieterlen (1971) in Kivu where *melanotis* is present. The ecological picture for *mesomelas* is similar in both studies, but it looks as though in Kivu *mystacalis* is entirely pushed out of the choicest habitats and is replaced by *melanotis*.

NUMBERS OF *DENDROMUS* SPECIES TRAPPED IN THREE HABITATS IN KIVU (FROM DIETERLEN, 1971)

SPECIES	Dry-grass savanna	Mixed biotope (<i>Pennisetum</i> and dry grasses)	Moist habitats (marsh, herbaceous growth, <i>Pennisetum</i> and montane forest)
<i>melanotis</i>	14 (24%)	34 (81%)	39 (85%)
<i>mystacalis</i>	23 (40%)	2 (5%)	0 (0%)
<i>mesomelas</i>	21 (36%)	6 (14%)	7 (15%)

DENDROMUS DENSITIES FOR 4 HABITAT'S IN HAUT ITURI (FROM MISONNE, 1963)

SPECIES	Grass savanna		Savanna with secondary herbaceous growth		Herbaceous growth bordering marsh		Marsh	
	a	b	a	b	a	b	a	b
<i>mystacalis</i>	0%	0 p.h.	0.6%	0.6 p.h.	15.2%	19.8 p.h.	3.8%	3.6 p.h.
<i>mesomelas</i>	8.9%	5.6 p.h.	5.1%	6.6 p.h.	0.4%	0.5 p.h.	0%	0 p.h.

a) percentage of total rodents and insectivores present.

b) density of numbers present per hectare.

The ecological and geographic distribution of the various *Dendromus* species might therefore reflect a hierarchy in which there are chronological implications and also scales of dominance.

D. mesomelas, which Misonne points out as the calmest and the least aggressive species, ranges through the widest variety of ecological zones. It tends to occupy the driest and most "terrestrial" habitats wherever other *Dendromus* are present but, in the alpine and subalpine zones of many mountains and in parts of southern Africa, it lives in very wet, grassy and herbaceous growth with the entire *Dendromus* habitat to itself. Perhaps this species has had time to adapt to most grassy habitats and is therefore an "older species".

That *nyikae* may be a true relic species is suggested by its sparse and scattered distribution in the southern savannas and woodlands.

D. melanotis has the most extensive geographic range and is the most successful and apparently dominant species. It seems to be the most able to cope with the exacting conditions of the African savanna.

D. mystacalis is more exclusively a climber and, in that sense, may be said to be the most highly evolved, although no species is so specialized as to be unable to live on the ground. It is a low-altitude species and is not found much above 2,000 m. Misonne includes in *mystacalis* the Congolese forest form *messorius*. Dieterlen, instead, regards *messorius* as a distinct species (but derived from *mystacalis*); he suggests that the very different *messorius* and *melanotis* subspecies meeting in the north-eastern and eastern Congo are possibly terminal links of a "Rassenkries" coming from the west and east. More material is needed to explore this interesting field of enquiry.

All *Dendromus* species make nests. There seems to be a correlation between the site for these nests and the species' habitat. *D. mystacalis*, in the wettest habitats, builds in rather exposed situations quite high up in rank vegetation, banana trees, etc; *D. mesomelas* builds at low levels and often uses birds' nests and also burrows among boulders; *D. melanotis* and *D. nyikae* are often harassed by annual fires and they both build nests underground in burrows; *D. melanotis* also builds nests above ground but seldom more than a metre from it.

Dendromus species are agile jumpers as well as climbers. I have mistaken *D. nyikae* for a small gerbil as it hopped along the ground at night. They can make vertical leaps of 45 cm when frightened. All species are primarily nocturnal.

The females have eight mammae and bear between three and eight young at a time.

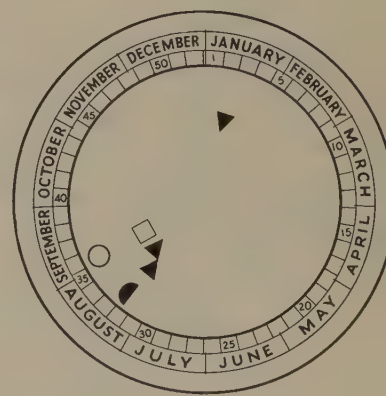
D. nyikae is the least known form. It resembles *D. melanotis* but is larger. It seems to be locally abundant in the "miombo" woodland zone but is otherwise rare over most of its range.

Hill and Carter (1941) list 63 specimens of *nyikae* from Chitau, in Angola, and only one other record from the very numerous localities in which mammals have been collected in Angola.

The breeding data presented opposite derive from six specimens I collected in one locality in southwestern Tanzania. Loveridge found a nest with eight young on Ukerewe Island in June. These took to sleeping with a gerbil in captivity, apparently treating it as a surrogate mother.

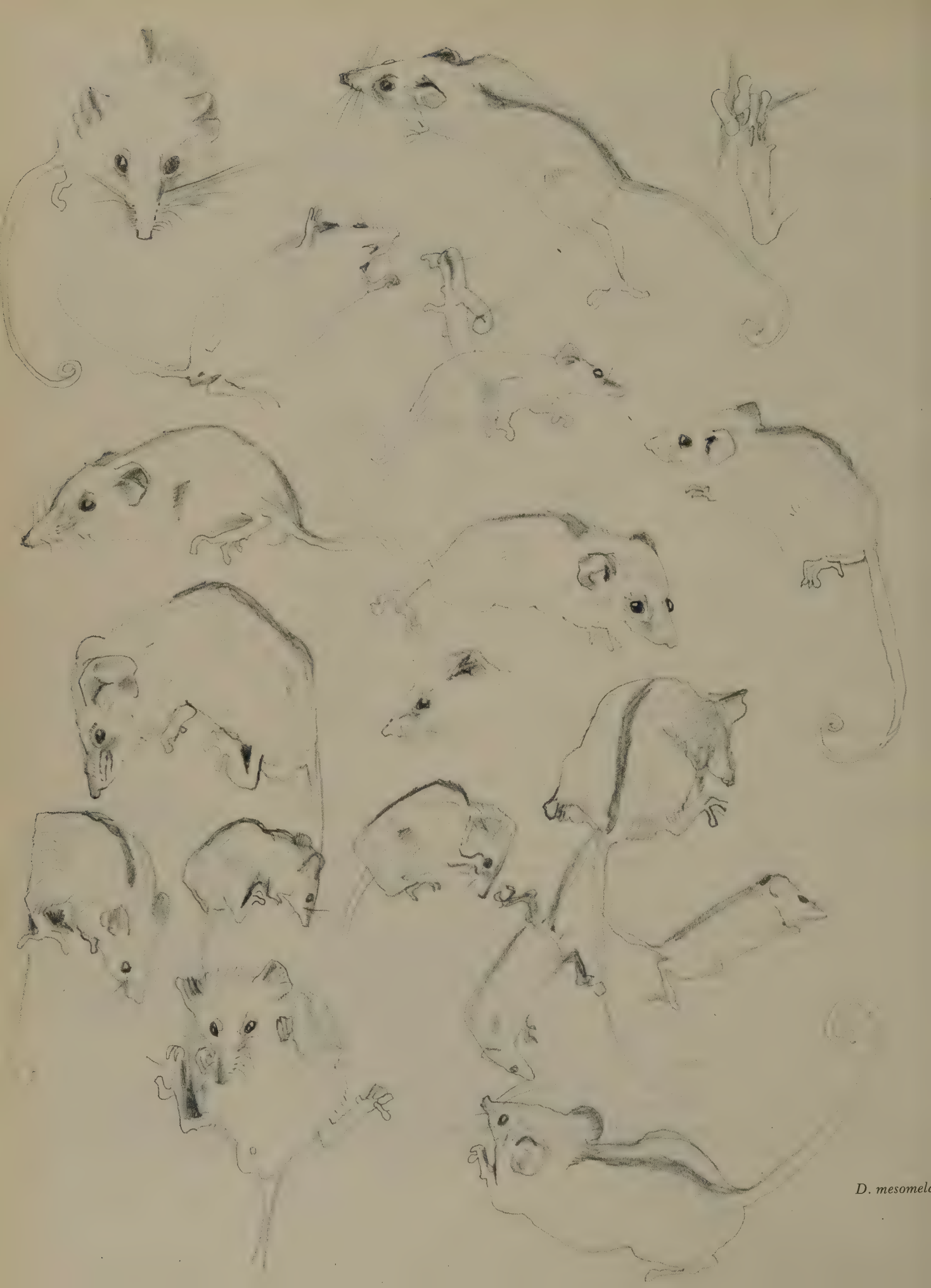
Over the greater part of its range *D. melanotis* lives in relatively open dry savanna, often in short grass and scrub growing on sandy plains. It is possible that the ecological range of this adaptable species is in the course of expansion for Dieterlen has collected this species in montane forest at 2,350 m in Rwanda. Of seven stomachs he examined three revealed a mixture of starchy and fatty seeds, one contained sorghum, another contained a mixture of seeds and insects and two others were full of small beetles. Shortridge (1934) stated that this species eats spiders, small lizards, young birds and eggs and Roberts (1951) reported that one *melanotis* even killed a small snake.

In areas where this species is subject to climatic fluctuations and fires breeding is probably strictly seasonal. Dieterlen has found that this species



Breeding records for *D. nyikae*.

- negative female.
- ▲ lactating female.
- ▲ male with large testes.
- male with testes not enlarged.



breeds most readily in captivity and was able to follow the development of the young, which takes 5 to 10 days longer than that of most other mouse-like rodents. He appropriately uses the ornithological term "nidicolous" to describe this character. He publishes an interesting comparison between the allometric growth rates of the tail relative to those of the head and body for this species and for *mystacalis*. The nests are well described in the notes of the Roosevelt expedition:

"made of long wiry grass, not lined and very small, less than three inches in diameter. They are globular and entered by a hole in one side, as with our marsh wrens. Only one mouse to a nest, as far as we saw; Heller caught two in their nests. The nests were in thorn-bushes, only about a foot and a half from the ground; once or twice these mice were found in what were apparently abandoned weaver-birds' nests. If frightened, one would drop out of its nest to the ground and run off; but if Heller waited quietly for ten minutes the mouse would come back, climb up the twigs of the bush, and re-enter the nest. It never stayed away long, seeming to need the nest for protection". (Roosevelt and Heller, 1915.)

Dendromus mesomelas is an upland species widely distributed in southern, central and eastern Africa with an isolated population in Cameroon. They live in various types of tall grass, feeding on grass seeds and insects. They spend much time on the ground, and in the high altitude grasses share the runs of *Otomys*. The nests are made both above and below the ground and this species often uses old birds' nests. This is the only *Dendromus* species that is known to be active by day as well as night.

They probably breed seasonally, as Loveridge caught many half-grown animals during late February in the Southern Highlands.

Dendromus mystacalis is a common and most successful species. It is also the most familiar, as it has adapted to cultivation quite readily and it is not unusual to find nests in garden shrubs, banana trees and banana bunches, in sweet potato vines, pineapples, palms and in thatched roofs. Their nests may be three metres or more from the ground but are generally lower down in thick herbaceous vegetation. Misonne found this species particularly numerous in the very common weed "namirembe", *Ageratum conyzoides*. Lang noticed that the solitary males' nests were smaller than those built by the females. The usual number of young is three or four, but as many as seven have been recorded.

Near the Equator there appears to be a birth peak between November and January, but there are scattered records in other months from the eastern Congo (Zaire) and Uganda.





Deomys, Link Rat
(Deomys ferrugineus)

Family Cricetidae
Order Rodentia

Measurements
head and body

120—144 mm

tail

150—215 mm

hindfoot

32—39 mm

weight

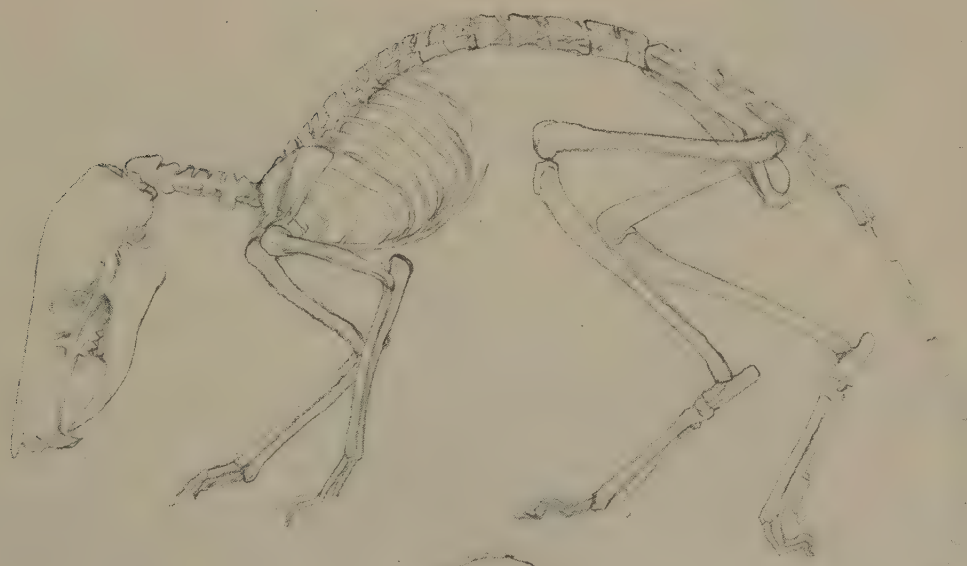
40—70 g

Deomys, Link Rat (*Deomys ferrugineus*)

Deomys is a highly distinctive species, unlike any other type of rat or gerbil. It has long legs and a most remarkably pointed narrow head surmounted by enormous ears. The bicoloured tail is very long and has a slight brush of white hairs at the tip. The underside is pure white. The upperside is a rich tawny orange, with longer darker hairs down the back and on the rump. These hairs are flat in section and slightly springy or bristly to the touch; when the fur is ruffled it reveals that the underfur is very pale grey and that only the tips of the hairs are pigmented. The roots of these bristle hairs grow in lines and create a granular texture in the skin.

The name "link rat" is a literal translation of the name coined by Thomas (1888). He thought this species represented a "missing link" between the cricetid and murid rodents because of the extra cusps on its teeth. Misonne (1969) points out that too much importance is sometimes given to more or less aberrant structures. He singles out for criticism Ellerman's proposal (1940) of a special subfamily of Deomyinae to hold this species. It is now generally accepted that *Deomys* is a highly specialized member of the Dendromurinae.

This is a true forest species which occupies the tropical forest between the Cameroon-Gaboon area and the Victoria Nile. In Uganda it has been found at low and medium altitudes but it might occur up to about 1,800 m. It seems to be commonest in or near seasonally flooded swamp forest. It makes leaf and fibre nests in holes or crevices at the base of trees and Bates (1905) saw one come out of a hollow tree that was being smoked.



A captive that I kept for a week added a few leaves each day to its rudimentary nest, which was inside a dark small box. This captive fed on grasshoppers, snails, millipedes and crickets, a similar diet to that found in the stomachs of trapped animals.



They eat insects (mostly termites) and arthropods, occasionally also vegetable matter. The oily pulp of the *Elaeis* palm nuts seems to be acceptable to several species that otherwise feed on animal foods. The table below shows the frequency of foods found in some of the stomachs of specimens from Uganda and the eastern Congo (Zaire), including Hatt (1940) and Rahm (1966).

Insects*	18	
Ants	8	
Crickets and grasshoppers	3	Frequency of food
Caterpillars	3	types recorded from
Beetles	2	<i>Deomys</i> stomachs
Slugs	2	
Oil palm nuts	2	
<i>Strombosia</i>	1	

* "Insects" probably stands for termites in most cases.

They have been reported to eat aquatic crustacea in the Cameroons, and Sanderson (1940) saw them wading in order to catch this prey. I have watched them in shallow water walk on tip-toe, keeping the body well clear of the surface; they have a rather dainty, fastidious air.

On the forest floor they snuffle over leaf litter with whiskers and nose twitching. The whiskers resemble those of a shrew in their length and density





and their sensory role must be as important as their sense of smell in finding food. Hearing may also play a part, judging by the altering position of the ear pinnae as the animal seeks its food. The forelegs are used to pull earth and other obstructions loose; any promising bit of tangled root, loose vegetable fibre or piece of bark is held down with the hands and torn apart with the teeth. If living prey is encountered, it is pounced upon and bitten several times with the incisors and is then torn apart and swallowed. The animal holds its prey down against the substrate and pulls bits away and swallows them. Chewing seems to be rather perfunctory and the small black elliptical slugs that are common in swamp forest are swallowed whole. If an active prey like a cricket escapes, the animal snuffles about feverishly and indulges in short bouts of frenzied grooming that are probably "displacement activity".

By contrast, normal grooming is a leisurely and prolonged affair. The animal sits on its haunches and is particularly careful to clean its hindquarters, rump, hindlegs and tail. The tail is passed through both hands and mouth in a very systematic manner, starting from the root and ending at the tip. Any dirty spot is given great attention until it is completely clean. The ears and face are rubbed by the forelegs and the legs are licked free of anything that rubs off onto them.

Deomys sleeps curled up lying on its side after turning round and round in the nest. Sanderson described animals bounding on their hindlegs like springs. It is true that *Deomys* can make great leaps, but these are the result of fear and cannot be described as a normal type of progression. The leap is sharply vertical, and can measure up to 50 cm in height; it is made very suddenly. There is no forewarning of the jump and it must be an effective means of escape.

Deomys can climb well, using only its toes and fingers and making great use of its tail as a counter-balance but never wrapping it round a branch for support. It may leap from one branch to another but the impetus of these horizontal leaps is very much smaller than when it leaps off the ground, and distances of more than 15 cm between branches are either not attempted or end in a fall to the floor.

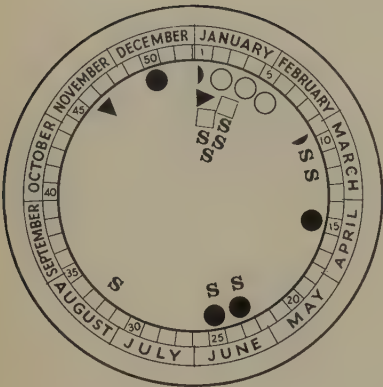
Hearing is obviously very acute, but the small eyes seem to register very little and a grasshopper out of range of the whiskers but in plain view of the animal is ignored.

Judging from the activity of a captive, the animal is crepuscular, with occasional bouts of activity in the late afternoon. This animal was also intermittently active during the night. I have once seen *Deomys* about by day in the forest, and Lang had animals caught in the early morning and evening (Hatt, 1940).

Deomys are not rare in the larger Uganda forests but they are seldom found in numbers, nor are they evenly distributed in the forest. Pairs have been seen together by Sanderson, and traps sometimes catch a male and female in close proximity, so that this association and that of mother with young seem to be the main social units.

Extensive trapping in Uganda forests has also shown that there are seasonal changes of range. The well-drained areas of secondary forest away from the rivers and streams are inhabited by *Deomys* during the rains, but they are not present there when it is dry, at which time they concentrate in the moist





Deomys breeding calendar.
 S subadult.
 ○ negative female.
 ▲ lactating female.
 ● pregnant female.
 ▲ male with large testes.
 □ male with testes not enlarged.



Deomys.

swamp forest areas. They are probably dependent on water and my captive drank frequently.

Their ecological niche is very close to that occupied by *Malacomys* and the relatively restricted range of *Deomys* might be due to competition with *Malacomys*. There can be little doubt that the latter is more recently evolved and is a more successful species.

There is in fact evidence suggesting that *Deomys* suffers in competition with *Malacomys*. The latter rodent is absent from the seasonal swamp forest at Sango Bay, a habitat that provides the sort of condition in which it would normally flourish. This forest is very ancient and it has suffered lengthy isolation from the main forest block (see Vol. I, p. 73 ; and Kingdon, 1971). That *Malacomys* has been unable to reach this forest is probably due to its evolution being more recent than the isolation of this forest.

The following table compares the status of *Deomys* and several other small rodents that are present in Sango Bay with their status in swamp forest in Bwamba, where *Malacomys* and its relative *Colomys* are abundant. The seven species selected are the only rodents likely to use the same or similar resources. Identical trapping methods were used in each locality.

SPECIES	SANGO BAY	BWAMBA
<i>Deomys</i>	28·5% (8)	5·05% (5)
<i>Malacomys</i>	0% (0)	21·21% (21)
<i>Colomys</i>	0% (0)	9·09% (9)
swamp forest rodents	28·5%	35·35%
<i>Praomys</i>	28·5% (8)	26·26% (26)
<i>Lophuromys</i>	10·75% (3)	17·17% (17)
<i>Hybomys</i>	14·25% (4)	12·12% (12)
<i>Hylomyscus</i>	18% (5)	9·09% (9)
TOTAL	100% (28)	100% (99)

The figures suggest that *Deomys* fills the *Malacomys* niche where that species is absent, but it probably competes less with the more aquatic *Colomys*.

Deomys seems to have very extended breeding peaks and might possibly breed throughout the year. That one litter can follow close on another is shown by one female being pregnant and lactating at the same time. The young number from one to three, with two being the most common number. The female has two or three pairs of abdominal mammae.

Hatt reports finding nematodes in one stomach.

Fat Mice (*Steatomys*)

Species

Steatomys pratensis

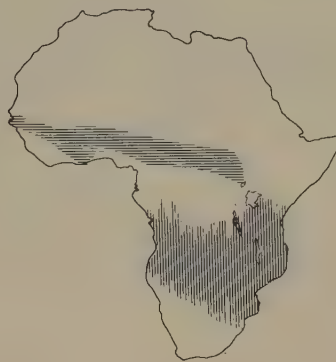
Steatomys opimus

Steatomys minutus

S. pratensis (includes *parvus muanzae* and *athi*), 10 to 14 mammae, white underside, sandy brown above with darker tone down the back. It is found in all savannas of sub-Saharan Africa.



S. pratensis.



S. opimus.

S. minutus.

S. opimus (includes *gazellae*) 12 to 14 mammae. It is found in the northern savannas.

Steatomys minutus (includes *loveridgei*) 8 mammae. It is found in the southern savannas.

There is still too little known about fat mice for individual profiles of the species to be drawn. There has not yet been any recognition of separate niches occupied by each species, so that the account which follows is necessarily rather generalized. Most observations refer to *pratensis*, which seems to be the commonest and most widespread species.

Steatomys are very widespread in savanna and woodland. They are locally abundant in certain localities, but apparently absent over very large intervening areas. They favour sandy and cultivated areas, rocky hills, open woodland and also the margins of grassy plains. The hardness of the soil is probably a crucial factor in the distribution of fat mice, for they dig deep burrows on which they are peculiarly dependent. These burrows slant steeply down to a depth of at least 40 cm and have been known to go down to well over one metre. The burrow is relatively simple with few passageways and it leads to a central chamber in which is built a nest of fine grass or shredded fibres.

Fat mice carry their food to the burrow to eat it. This habit may be more of a reflection of the animal's vulnerability than an insurance against hard times, for the food is not stored for long and there may be more of an accumulation of discarded food debris in the burrow than whole seeds.



Fat Mice (Steatomys)

Family Cricetidae
Order Rodentia

Local names
Ntundu (Chimambwe)

Measurements head and body

50—100 mm

Steatomys pratensis

tail 33—55 mm

hindfoot 13—18 mm

skull 20—26 mm

head and body

100—140 mm

Steatomys opimus

tail 52—72 mm

hindfoot 18—20 mm

skull 25—30 mm

head and body

60—89 mm

Steatomys minutus

tail 33—45 mm

hindfoot 13—17 mm

skull 21—23.5 mm

Steatomys, like *Dendromus*, are primarily seed-eaters but fat mice are very adept diggers and bulbs, groundnuts and insects are also eaten. They eat the seeds of short-stemmed *Eleusine* and pick up fallen seeds from the millet fields. They have been known to eat grass.

Roberts (1951) described their response to being dug out. "They dig away, blocking the passage behind them as they go and if pressed they dig upwards until they break the surface and flee".

The most peculiar feature of *Steatomys* is its capacity to lay down very thick fat deposits all over the body, beneath the skin and around the viscera, and reduce its body temperature and activity, at which time it can survive on minute quantities of food, reducing its energy requirements to a minimum.

Petter (1966c) measured the rectal temperature of *S. opimus* kept in Paris and found that, when in a state of lethargy, they were incapable of movement and their temperatures were little higher than that of the room they were in (20°C—27°C). These mice were active for about one hour each evening, at which time their temperatures rose to 33°—34°C. This peculiar activity pattern was kept up by one animal for two years, during which time there was no loss of weight, in spite of the daily intake of food amounting to just a few grammes.

Vesey-FitzGerald (1966) found *pratensis* common in old fallow cultivation and in sandy places in the upland secondary grassland of the Ufipa Plateau. The loosened soil of cultivation favours their spread, but this is offset by their being a choice tit-bit in local stews, so that they are becoming scarce in some areas.

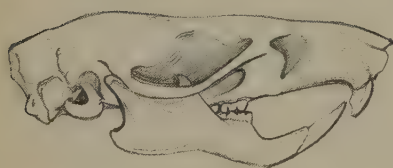
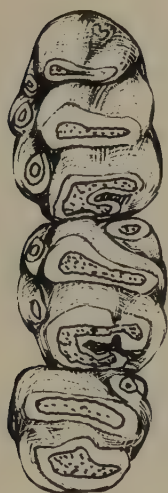
Fluctuations in the fat deposits of fat mice have been noticed in several parts of Africa. Animals collected by Vesey-FitzGerald in October, at the end of the dry season, were very fat. Near Mbeya I found very fat animals in September, November and December. In November one female had 3 small embryos. Under the similar climatic and ecological conditions of northern Zambia, Ansell (1960a) records a pregnancy in December and another in April.

Pouched Rats and Mice

Cricetomyinae



Cricetomys with distended cheek pouches.



Tooththrow and skull, *C. gambianus*.

The pouched rats and mice are a small but interesting group of rodents sharing several well-defined characteristics.

Large cheek pouches are possessed by all the three genera included in this subfamily: *Cricetomys*, *Beamys* and *Saccostomus*. This anatomical peculiarity is linked with the habit of food collecting, the pouches serving as a sort of "shopping basket" for the animals' forays after food. All species dig burrows in which there are storage chambers where the food is eaten at leisure. They also have a tendency to "camp", digging holes very close to their food and moving when the supply is exhausted.

All genera have grey or greyish-brown colouring and are slow in their movements and unusually tame, generally only biting if bullied. However, once frightened they may stay in their burrows for 24 hr.

The habit of storing food is generally an adaptive precaution against lean times; this has yet to be shown to apply to any of the Cricetomyinae for they appear to store throughout the year. With the possible exception of *Saccostomus* no species is normally subject to severe seasonal changes and the adaptive advantage seems to be efficient gathering of food into the home shelter where it can be eaten in safety, rather than an insurance against seasonal shortages, although this may also play a part. *Cricetomys* continue hoarding even after collecting enormous stores.

The pouched rats and mice make underground nests and even have separate latrine chambers so that relatively long periods can be spent within the shelter of the burrow. A female *Cricetomys* studied by Ewer (1967) spent 2 hr in 24 away from her home cage while a male was abroad for a total of only 4 hr.

Compared with the immensely successful rats and mice, this subfamily is almost certainly a relatively ancient group which, in spite of their extraordinary slowness and tameness, has survived through specialization.

The secret of their survival in competition with alert and agile murines and in the face of predation would seem to lie in their "camping" food-gathering existence. The primary advantages of their food storing behaviour might therefore lie in diminished exposure to predators and in more rapid harvesting *vis-à-vis* other rodents. Captive giant rats, for instance, will move food to their store very speedily. An animal returning to a shared nest with food stimulates the others to go out and collect. In spite of a low reproductive rate success is probably improved by longevity. Captive *Cricetomys* live for over 4 years.

An interesting commensal relationship has developed through the habit of storing food. A type of cockroach, *Hemimerus*, has adapted to live off the stores. The most primitive form associated with *Beamys* appears to live mainly in the nest and it is rarely found on the animal. The more advanced species, *Hemimerus talpoides* and *Hemimerus hanseni* actually live on the body of *Cricetomys*.

Lesser Pouched Rat (*Beamys hindei*)

Races

<i>Beamys hindei hindei</i>	Kenya Coast and northern Tanzania
<i>Beamys hindei major</i>	Southern Tanzania and Malawi

Beamys resembles a smaller *Cricetomys* and has a similar white-tipped tail but this is usually marked with blotches instead of having a sharp change from dark base to white tip. The fur shows three distinct colour phases—a soft, light-grey in juveniles and subadults, a darker grey in adults, and a brownish adult phase, which appears as a reddish tinge and may spread over the body or remain restricted to the rump and sides. Brown animals become grey again and the change may be a seasonal one.

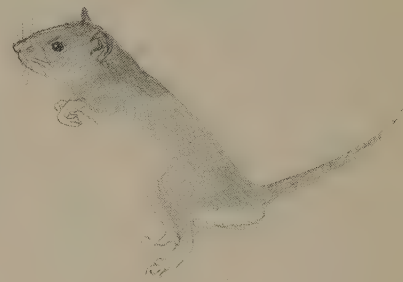
Beamys is a relic species surviving in the “southern forests” of eastern Africa (see Vol. I, p. 71). It is probably close to the ancestral stock of *Cricetomys*. Its habitat is forest and moist woodland from sea level up to 2,100 m. Soils need to be soft and sandy as it lives in burrows that it digs itself. It must also live near water; indeed this rat could almost be termed a bank-dwelling species because of its need to be within easy reach of a source of water. Captives have been found to die without water.

The burrows of *Beamys* resemble those of *Cricetomys*. There is a vertical shaft which is plugged at the bottom, passages with enlarged chambers for nesting and storing food, and there is at least one cul-de-sac, the end of which is used as a latrine. The nest is made of dry leaves and other vegetable debris and the materials are changed regularly. Burrows are enlarged from time to time and new chambers and passages are added in a more or less linear progression. Burrows are about 60 cm deep and may extend up to nine metres in length.

The food consists mainly of seeds and fruit. Hanney and Morris list the seeds of *Mucuna aterrima*, *Erythrophleum guineense*, *Strychnos*, *Cassia* and *Vigna urgulculata* as well as the stones of mango (in a very high proportion of burrows) of avocado pears, the seeds of tea, passion fruit, maize, oleander and cassava and the fruits of Persian lilac, *Melia azedarach*. Captives also ate parts of a spiny mouse, *Acomys*, and a chameleon.

Enormous activity is expended on food collection throughout the year. Hanney and Morris (1962) calculated that one store they excavated represented a minimum of 200 forays. On the other hand, burrows were well placed and all foods were available within 36 metres. The debris of food eaten in the burrows is collected and removed quite regularly and food waste more than three days old has not been found underground.

The rarity of *Beamys* in collections and its late discovery (Thomas, 1909) are due to its being very trap-shy. In an area that was systematically trapped over the greater part of a year I caught only two subadult animals. Hanney and Morris caught a single rat with a cheese-baited trap, depending upon excavation to catch the rest of their series of 25 animals. When exposed, *Beamys* makes little effort to escape and is generally tame from the start.





**Lesser Pouched
Rat**
(*Beamys hindei*)

Family Cricetidae
Order Rodentia

**Measurements
head and body**

130—187 mm

tail

100—155 mm

weight

55—150 g

Although slow it is a confident climber and harvests some of its food still attached to the plant; the tail is wrapped round branches and provides support in climbing.

The tail might also serve as a visual signal for it is held stiffly upwards while the animal stands on its hindlegs in an attitude of curiosity.

They are completely nocturnal and captives rarely show any activity during the day.

Burrows are occupied by a single animal, except when the female is with young, but the burrows of a male and female are sometimes merely a few metres apart. Burrows are very seldom isolated and they usually occur in groups.

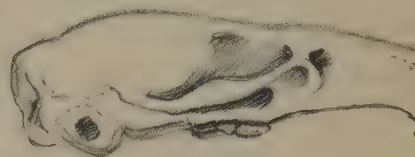
Hanney and Morris reported serious fighting amongst captives put together in one cage; one adult female killed and partly ate two subadults put in with it.

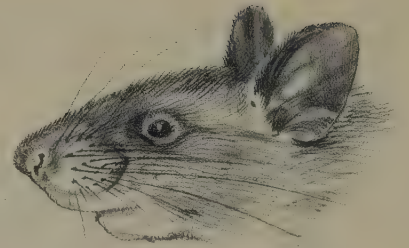
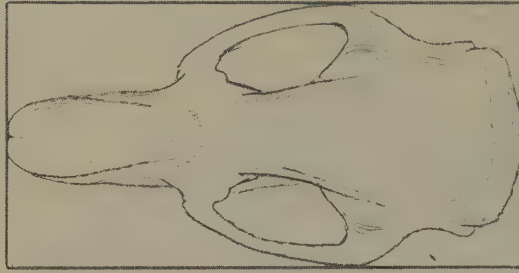
Although *Mastomys* may use old *Beamys* burrows no other rodent lives in close association with this species. Their habitat is shared by many rodents, *Praomys* and *Aethomys* being particularly common and dominant species. *Thamnomys* species probably share their arboreal habitat.

Hanney and Morris found *Beamys* parasitized by the flea, *Dinopysyllus lypusus* and by *Cordylobia* maggots in the groin. A more primitive form of cockroach than that found on *Cricetomys* was found in the nests but not on the animals. The apparent restriction of *Hemimerus* to the burrow is very interesting as it suggests that the highly developed association where *Hemimerus* lives on the body of *Cricetomys* started as a simple commensal relationship where the insect used the rodent's food store. Since Ashford (1970) has found that one species of *Hemimerus* (*talpoides*) shows no interest in the food of *Cricetomys gambianus* but feeds on the secretions of the rats' skin, a comparative study of these two rodents together with their commensal cockroaches would be of great interest. The near ancestral status of *Beamys* (and presumably of its species of *Hemimerus*) offers an unusual opportunity to explore the evolutionary development of a unique relationship between a mammal and an insect.

In Malawi breeding has been found to coincide with the rains. Populations in southwestern Tanzania under a similar climatic regime to that of Malawi can be expected to follow the same pattern.

Between four and seven young are born at a time. They live in the mother's burrow until they are about 105–122 mm long (head and body). They then leave to dig their own burrows. By the time the animal is 136 mm long it is capable of breeding. *Beamys* resembles *Cricetomys* in having a very wide range of adult sizes and weights.





Cricetomys gambianus

Primarily savanna



Cricetomys emini

Forest

Giant Pouched Rats (*Cricetomys*)

Family
Order
Local names

Cricetidae
Rodentia

Buku (Swahili), Kayonzi, Nsomba
byuma (Luganda), Msumba
(Lubwizi, Lutoro), Káyozi
(Lusoga), Livunzi (Gisu), Erunge
(Kitosh), Impenga (Ishinuyha),
Benha (Kinyakyusa), Adube
(Kuamba), Epude (Karamojong),
Isisa, Eichidje (Lukonjo), Azitya,
Ekorikituk (Itesot), Lakwalpala
(Lwo), Unget (Kimasai), Keriang
(Kisebei), Kikomi (Luhya)

Measurements
head and body

280—450 mm

tail

365—460 mm

weight

1—1.47 kg

Giant Pouched Rats (*Cricetomys*)

The two species of giant pouched rat are of similar size and are difficult to tell apart. The most obvious difference is the soft grey coat of the forest *C. emini* and its clean white belly; *C. gambianus* has coarser, browner fur and a dark mask round the eyes.

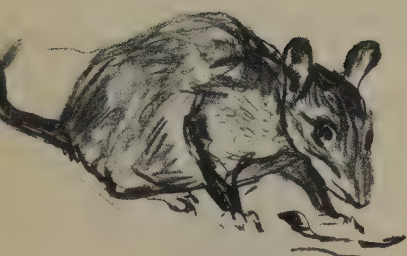
C. emini is exclusively a forest species and in East Africa is only found in Uganda, where it is sympatric with *C. gambianus*.

Bourlière (1948) attempted to hybridize the two species but failed and Genest-Villard (1967) comparing the two species in captivity discovered important vocal differences that would probably make communication between the species difficult. *C. emini* has a long modulated call whereas *C. gambianus* makes a short single cry. In Bwamba, where both *C. emini* and *C. gambianus* live side by side, the character of each species is well defined and there are no intermediate forms to imply hybridization. It would be interesting to know if there is any behavioural mechanism other than the voice serving to isolate the two species reproductively.

This profile is drawn mainly from observations of *C. gambianus*: significant differences in behaviour may therefore have been overlooked.

C. gambianus occurs in almost all habitats south of the Sahara but it does not extend further south than the Transvaal and Zululand. In arid open country it may be rare or absent, but where there are riverine thickets or rocky hills, the giant rat may find a living in otherwise rather arid country. They are reported to occur up to 3,500 m on Mt Elgon and are common on Ruwenzori up to about 2,100 m. They are primarily nocturnal and die rapidly if exposed to excessive sunlight or heat, so that shelter is most important. Often the giant rat uses natural crevices and holes, termitaries, hollow trees and eroded root systems but it is capable of digging its own burrow. This may





consist of quite a long passageway with various side alleys and several chambers, one of which may be used as a sleeping place or breeding nest, another or others as stores. Here food such as beans, roots, bulbs or nuts are kept after being brought home in the very capacious cheek pouches. Of cultivated plants, cassava, maize, groundnuts, beans, mango, palm nuts and avocado pears are eaten. Sweet potato tops are consumed by both species in captivity; bark and termites are also eaten. Rahm and Christiansen (1963) list some foods taken by *C. emini* in eastern Zaire (Congo): the fallen seeds of *Carapa* and *Syzygium* and the leaves of *Basella alba* and of *Galinsoga parvifolia*; they also report snails as an important food for this species. The giant rat is coprophagous and is dependent on water or, at least, moist food.

The stores also contain many non-edible objects, apparently selected for their glitter. Some local names refer to this habit, "Nsomba byuma" is "metal thief" and "Lakwal pala" is "knife thief". A list of objects found in *Cricetomys* burrows reads like the inventory of the pockets of a kleptomaniacal schoolboy: knife, bottle-top, key, pencil, pen, chalk, silver earring, blue glass marble, red cloth, ring and 300 francs in coins.

The addition of these odd objects to the food store suggests that carrying, whether in the teeth or in pouches, is rewarding in itself. While the impulse to carry may be discharged at other objects by an absence of food, Ewer (1967) has shown that a succession of journeys to an abundant food source eventually seems to exhaust the rat's drive to fill its pouches with food while the impulse to carry may be longer lived. Thus the last burdens of a collecting session are often eccentric in spite of food still being available and hoarding is betrayed as behaviour containing distinct components beyond the purely appetitive (see Ewer, 1967). A rat may spend $\frac{1}{2}$ —6 hr hoarding and it may make 10—100 trips. A captive rat collected nearly 3 kg in 38 trips over $2\frac{1}{2}$ hr. The pouches can contain about 100 ml at a time and Ewer found that the more difficult the trip the fuller the pouches and the fuller the pouches the less delay returning. The margin table opposite illustrates this tendency.

Both *Cricetomys* species climb quite well and I have seen one clambering upwards about two or three metres in a mimosaceous tree; Eisentraut (1963b) also reports shooting one out of a tall tree. They can jump reasonably well and also swim. I noticed a curious inhibition in a captive *C. emini* which was kept in a very large box, in the lid of which it had gnawed a hole. It emerged at night on the top of its box and yet it never tried to jump or climb down to the ground, a distance of less than two metres, although this was clearly well within its capacity. Could it have been the alien smells of its surroundings that made it stick to its box?

In captivity adult males put together may fight and often dribble urine while doing so. Urine trailing also tends to be a male function as does cheek-rubbing. Males also deposit dung while assuming a highly ritualized hand-stand position. All these ways of scenting the habitat suggest territorial marking behaviour. It is uncertain whether saliva or other secretions are involved in cheek-rubbing but it is frequently conducted while the rat stands on its hindlegs. Threats are also made in a vertical posture with teeth-snapping and the pouches puffed out. However both sexes assume an upright stance when peering around and also in the first stages of courtship.

They are usually found singly and the males in particular are largely soli-



tary animals. Rousselot reported aggregations of females with young consisting of up to thirty animals, all living in the same burrow system. This is probably rather rare and must depend upon a very large food supply. A tendency that has been widely observed is for *Cricetomys* to change its burrow quite frequently. This may be influenced by the availability of food for, where possible, this rat lives very close to its food supply.

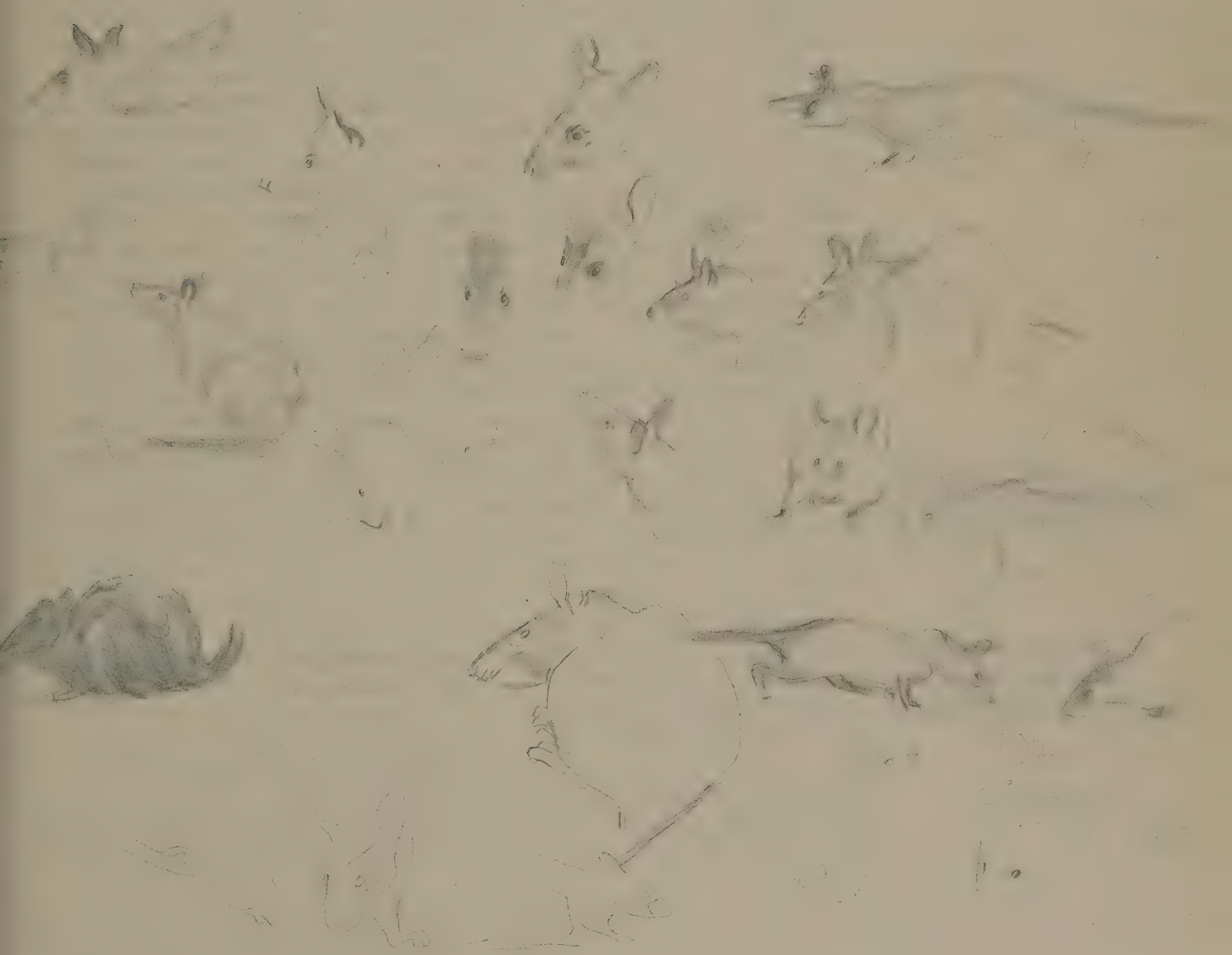
On a farm in southwestern Tanzania a coffee store became tenanted by a giant rat while an avocado and a mango tree were fruiting outside. The rat made its nest of sticks, leaves and dried mango stones, beneath a pile of sacks, and went out each night to collect the fallen fruit that lay a few metres away from its nest.

A very interesting parasite lives on *Cricetomys*. This is a flightless cockroach, *Hemimerus*. One species *H. hanseni* is reported to feed on the stored food and debris in the rat's burrow, but Ashford (1970) observed *H. talpoides* feeding only on the rats' body secretions. Seven or eight of these insects live on each rat.

Reports of giant rats being killed and eaten by carnivores seem to be rare. Chapin (1932) reports one eaten by an eagle, *Aquila nipalensis*. Bourlière

	close,easy journey	more difficul journey
Session	4hr 23min	4hr 59min
No. of trips	96	77
Vol. of maize	4,250 mL	4,675 mL
Pouch load	44.7 mL	60.6 mL
Homeward delays	27	10

Food hoarding behaviour. Data after Ewer (1967).



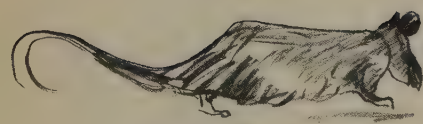
(1955) reports that an adult pair of giant rats violently attacked a python that was put in a cage with them. Their young one on the other hand appeared to be completely indifferent to the snake, even sniffing its nose.

By far the most important predator of this animal is man. The eating of giant rats is dying out in some areas, but they are still relished in many regions and Hatt (1940) reported that in the then Belgian Congo some attempt had been made to breed these animals commercially as food. They are certainly easy to keep and are common in zoos where they have lived up to four and a half years. In some West African towns giant rats have become sufficiently urbanized to invade the sewers. On small holdings they are a nuisance, as they cause some damage to beans, cassava and groundnuts. In Ruwenzori and in some other areas their skins are used as tobacco pouches.

The courting male makes a curious piping call; he may find the female on the defensive and mating is often preceded by both sexes rearing up to face one another in the fighting position. However, neither animal bites and the female may be shuffled around on her hindlegs for some time. Eventually the male grooms and cheek-rubs the female until she allows copulation. Gestation is about 32 days and captive females become very aggressive at parturition. One to four young are born, naked and with eyes and ears closed. Fur becomes perceptible on the fifth day and the young animal becomes well-furred by the third week. The eyes open and mobility begins during the fourth. At the age of twelve days there are outbursts of violent fighting when the young are alone in the nest; this becomes more playful a week later. The tail is initially rather short and Ewer noted a sudden burst of tail growth at 30—35 days. Captive males are tolerant of the young but often move them out of the nest. Ewer noticed that the female altered her choice of foods before the young were weaned, softer foods becoming more attractive. At about the same time the young start to feed on the mother's pellets. After weaning, competition for food is keen and the first use to which the pouches are put by the young is as safes to stop food being stolen. Ewer offered a youngster rice while the parent rats slept nearby "without waiting to take what she had been given, she whipped round and grabbed at her father's face, clearly expecting to find he also had a supply to steal which had first priority."

Although development is markedly slower than in the murid rats the female is sexually mature by the age of six months and may have her first litter at seven months.

Bourlière (1948) and Ewer (1967) give detailed accounts of the development of the young.



Pouched Mouse (*Saccostomus campestris*)

Family

Cricetidae

Order

Rodentia

Local names

Lokuuku (Karamojong)

Measurements head and body

115—188 mm

tail

30—78 mm

hindfoot

20—25 mm

weight

40—85 g

Pouched Mouse (*Saccostomus campestris*)

The pouched mouse has a round fat body, enormous cheek pouches, grey or brownish-grey colouring and short legs and tail. The teeth are without grooves. *Saccostomus* is well represented as a fossil in the Pleistocene beds at Olduvai.

As with its relatives *Cricetomys* and *Beamys*, *Saccostomus* is very variable in size and it may also have colour phases similar to those found in *Beamys*. Races or even species have been erected on the basis of size and colouring but in view of the known variation of *Saccostomus* these names are ignored here. Only detailed study on living animals and much more extensive collecting can reveal any meaningful pattern in the regional and individual variation of this species.

Saccostomus campestris has a typical southern savanna distribution, ranging over the whole of southern and eastern Africa. Pouched mice can be found in various savanna types. In southwestern Tanzania, Vesey-FitzGerald (1966) found them more frequent in areas where herbage is in decline and subject to annual fires. They often dig their burrows near stream beds but in view of the semi-arid areas in which they have been collected they can evidently be independent of water during the dry season.

They use holes dug by other rodents as well as digging their own. A fondness for making their burrows in cultivated land is probably due to a need for reasonably soft soils, as their paws are not specialized and burrows are essential to their survival. The burrows are generally of a simple type, often with two entrances and containing a single enlarged sleeping and storage chamber.

Large quantities of food are collected in the capacious cheek pouches and taken back to the burrow to eat. It has not been recorded what type of phasing is followed but it should be relatively easy to establish how frequently food is sought under various conditions, what quantities of food are stored and how long these stores can last. In any event, food pouches seem to serve as "shopping baskets" and food is only actually eaten in the shelter of the home burrow. *Saccostomus*, in common with other cricetomyids, is essentially a camping food-gatherer.

The food consists of dry seeds, berries and occasionally insects, notably termites. Vesey-FitzGerald found that cultivated beans were a favourite food in the Rukwa area and noted that most of the seeds collected belonged to the Leguminosae. The germinated seeds of *Colophospermum* are eaten in Zambia and *Acacia* species seeds are probably an important food in many areas. They forage mostly for fallen seeds, although they may also clamber about in short matted vegetation. They cannot climb trees, shrubs or grass.

The pouched mouse is singularly slow and one would have thought it hopelessly vulnerable to predators. It uses paths under the grass in common with other rodents and the Roosevelt expedition caught them on indistinct runways in long grass along dry stream beds.

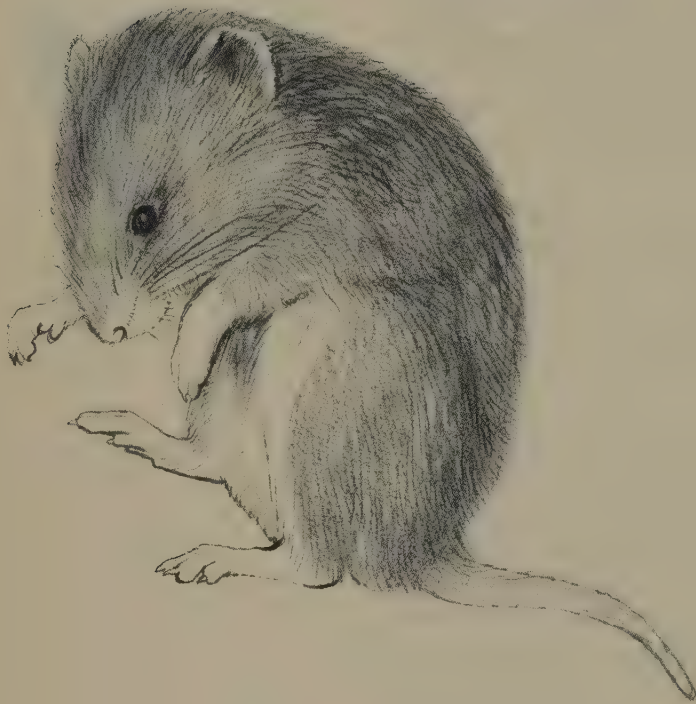
Never found in dense populations and also relatively rarely trapped, surprisingly little is known about *Saccostomus*. Ansell (1960a) thinks it might be communal, Copley (1950) thinks solitary. It is probable that the social struc-



ture resembles that of *Beamys*, for burrows are often in close proximity but each hole contains only one animal.

The female has ten or twelve mammae and bears up to eight young. Davis (1963) reports that careful management is necessary in captive pairs to avoid the killing of the male by the female when she is in oestrus. Juveniles and subadults have been collected in all seasons.

Saccostomus has been used as a laboratory animal at the Medical Research Centre in South Africa. It has been established as a regular breeder and has been found suitable to maintain *Schistosoma haematobium*.



Petromyscine Mice

Petromyscinae

This subfamily was erected by Petter (1967) to accommodate two rare relict mice, *Petromyscus* and *Delanymys*.

Although very different in appearance and habitat, the rock mouse of South-west Africa, *Petromyscus*, and the montane *Delanymys* share a similar molar structure.

Lavocat (1964) describing the phylogenetic importance of these rodents says

"*Petromyscus* and *Delanymys* are perfect structural links between *Mystromys* and the typical Dendromurinae and show us the clear systematic affinities of these forms. The presence of the characteristic Dendromurine third internal cusp on the molars in such an animal as *Delanymys* gives new and decisive proof that in the Dendromurinae the third tubercle is not the remaining part of a murid tooth but the newly elaborated structure of a cricetid tooth . . . thus *Delanymys* gives excellent supplementary proof of the close systematic connection between the Cricetodonts and the Dendromurines".



Left superior tooththrow in: left, *Cricetodon altasi* (after Lavocat, 1964); middle, *Delanymys brooksi* (after Hayman, 1962a); right, *Steatomys pratensis*.



Delany's Mouse
(*Delanymys brooksi*)

Family Cricetidae
Order Rodentia

Measurements
head and body

50—61 mm

tail

87—105 mm

hindfoot

17—19 mm

weight

5 g

Delany's Mouse (*Delanymys brooksi*)

This very small long-tailed mouse has long hindlegs with five mobile fingers and a vestigial thumb. The fur is dense and soft and of a reddish-brown colour, and it is interspersed with long stout guard hairs. The underside is buff with a tuft of white hair around the genitals. There is a distinct black spot between the eye and the nostril.

Most specimens of *Delanymys* have been collected in the Kivu-Bufumbira area of eastern Congo (Zaire), where most, but not all, animals have come from vegetation associated with high altitude marshes. This area is incredibly rich in endemic species. *Delanymys* undoubtedly represents a declining relic species now restricted to the mountainous heart of the Central Refuge, but there is also some evidence that it is relatively specialized. Hayman (1962a) suggests that it shows some convergent resemblance to the birch mice, *Sicista* (Zapodidae).

This suggestion has since been proved by Dieterlen (1969) to be very accurate as studies of numerous captives have shown *Delanymys* to be an active climber using its semi-prehensile tail and opposable toes to clamber about on slender stems. Hayman's recognition of the unique status of this mouse is particularly creditable because Chapin and other collectors had in fact collected some specimens as early as 1935 at Kashwa, at Tshibati in 1954, and at Lwiro in 1958, but they had been assigned to museum drawers containing *Mus* or *Dendromus*.

These animals are extremely trap-shy and I have shared the failure of other collectors (i.e. Rahm, 1967) to catch this rodent in snap-traps in spite of prolonged trapping programmes in appropriate habitats. Dieterlen has also failed to catch a single specimen in a snap-trap but has collected 26 animals by systematically clearing small enclosures, a method he calls "einzaunungs-fange" or fence-trapping.

Delanymys have been caught between 1,700 and 2,625 m altitude and Dieterlen has found them commonest along the borders of marshes where there is a very rich variety of sedge and grass species. Like *Dendromus* they are grass seed-eaters, but stomach contents have revealed only a pale homogeneous pulp of well-chewed vegetable matter. The absence of husks has led Dieterlen to think that only the inner parts, or perhaps unripe seeds are eaten, probably directly off the stem. Verheyen (1965) found traces of fruit or berries in one stomach. Dieterlen's captives fed almost exclusively on sorghum and were easy to maintain on this diet, one living as long as 15 months. A curious habit he observed was that they defecate in their water supply. Urine might be used for marking and Dieterlen points out that the long brush of urogenital hairs may serve to paint urine or glandular secretions onto vegetation.

He estimated that *Delanymys* was the fifth most common rodent in the swamp-edge vegetation around Lwiro (Zaire) and that there was a statistical chance of capturing one animal in 500 sq. m of the appropriate habitat. In



Kigezi, *Delanymys* may be a good deal scarcer for I chanced upon a useful indicator of nocturnal small mammal fauna in the form of owl pellets.

The grass owl, *Tyto capensis*, is common in Echuya Swamp (the type locality for *Delanymys*) and I have found there a cache of over 60 pellets. Although shrews were the predominant item in the owls diet, there were also large numbers of rodents. Yet there were no *Delanymys* remains.

If the superior hunting technique of the owls did not capture this rodent it must be either very rare or largely diurnal or perhaps both. There is evidence that the latter is not the case, for Dieterlen's captives are described as being active by night.

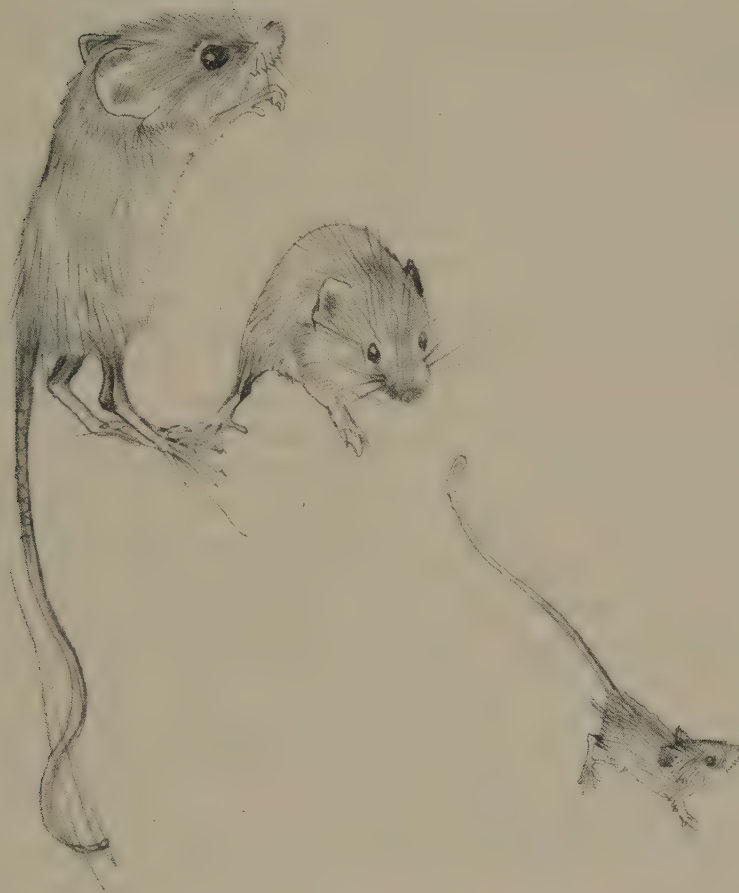
His records of small mammals associated with *Delanymys* are very interesting because they may throw some light on why this "living fossil" has survived. It is possible that the arboreal niche in tropical Africa may not be completely "saturated" and may still contain unexploited possibilities for small rodents, particularly at higher altitudes where cold temperature can severely limit or even exclude some otherwise successful climbers. In a swampy habitat, densely overgrown with a wide variety of plants, it is perhaps not surprising that climbing rodents are a dominant element of the small mammal fauna. However *Dendromus*, the most obvious competitor, is modestly represented by one common species, *melanotis*, and the generalized *Praomys* (*Hylomyscus*) does not feature in the list of important species at Lwiro. It does look as though in this particular locality a very rich three-dimensional habitat is being used by a rather small range of species, thus leaving room for an animal that might otherwise be competitively inferior.

The outcome of any direct competition with the very aggressive and specially adapted *Dendromus* cannot be doubted, particularly bearing in mind Dieterlen's remarks on the mild nature of *Delanymys*, instanced by its docility in the hand and the quiet co-existence of two captive males with a female. It should be remembered, however, that the minute size of *Delanymys* allows it to exploit very thin stems without competing with *Dendromus* even though it has less specialized feet and limbs.

NUMBER OF SMALL MAMMALS FROM SWAMPY
HABITAT NEAR LWIRO (FROM DIETERLEN, 1969)

<i>Terrestrial species</i>		<i>Climbing species</i>	
<i>Dasymys incomtus</i>	41	<i>Oenomys hypoxanthus</i>	109
<i>Otomys irroratus</i>	22	<i>Grammomys surdaster</i>	8
<i>Lophuromys flavopunctatus</i>	32	<i>Dendromus melanotis</i>	23
<i>Mus</i> species	12	<i>Delanymys brooksi</i>	22
6 other species	20		
(7 insectivore species)			
Total terrestrial rodents		Total climbing rodents	
	127		162

Three or four young are born in a very small, round grass nest which has one entrance. One nest found by Dieterlen in early June was 50 cm above the ground and was anchored by grass stalks to the branches of a bush; it contained four blind young.



Groove-toothed Rats

Otomyinae



The exclusively African Otomyinae resemble the Holarctic voles, Microtinae. While much of this resemblance must be due to the convergence of forms filling a very similar niche, it is also possible that both the Microtinae and the Otomyinae share an ancient common ancestry rather than having derived independently from separate Eurasian and African stocks of unspecialized cricetine rodents. Certainly there are no African rodents that could share any more recent common root. The teeth of Microtinae are not as highly specialized as the Otomyinae but their skulls and the general morphology of voles show a striking similarity.

Further interesting comparisons can be made between the ecologically equivalent voles and *Otomys*. Both are grass and herb eaters, living in runways under dense cover. As well as providing a vast food supply this herbaceous growth shelters them from climatic extremes and also from predators and is essential to their existence.

Voles are abundant over vast areas of the temperate region. In Africa, *Otomys* are commonest in temperate South Africa, but various species are also found in restricted humid localities throughout the eastern half of Africa.

I remarked in Volume I (p. 61) that *Otomys denti* has a relic distribution on a few widely separate mountain massifs. This was contrasted with the abundance of fossil *Otomys denti* throughout the Pleistocene. Discussing vegetation (p. 38) it was pointed out that grasslands are derived through three principal factors, fire, grazing and edaphic conditions. There can be little doubt that African grasslands have undergone great change and have also been greatly extended through the use of fire by pastoralists.

Otomys has probably tended to become a relic group because it is adapted to a "pre-fire" regime. Most *Otomys* species find survival difficult once the grass cover is burnt off. The grass types in which *Otomys* species flourish best are those in which fire only plays an occasional or a marginal role, and such habitats in East Africa tend to be at higher altitudes or in areas that are reasonably moist throughout the year.

Most *Otomys* species cannot be told apart except by referring to their teeth (and even then individual variation creates confusion). Nonetheless there appears to be some sort of an adaptive radiation within the genus. Rahm (1967) describes the ecological preferences of *Otomys irroratus (tropicalis)* and *Otomys denti* in the eastern Congo (Zaire). The latter prefers dense secondary growth associated with forest, whilst *O. irroratus* has a wider range of habitats from marsh to high altitude savanna and cultivation. However, Misonne (1963) has observed a very interesting change in the balance of these *Otomys* species on Ruwenzori. According to early collectors *Otomys irroratus* used to be the dominant species, but Misonne was unable to find this species and only captured *O. denti* in a very comprehensive rodent survey in the western Ruwenzori area. The genetic distinctness of these two species is probably of ancient standing and their relationship on a broader scale is also interesting. *Otomys irroratus* has sufficient ecological plasticity to co-exist with *O. denti* in certain diversified highland habitats within the Central Refuge area and

also in the moist "pseudo-savannas" of southern Uganda. In some other areas the Ruwenzori situation reported by Misonne could be seen as having been pushed to its conclusion long ago. On the geologically ancient mountains of Tanzania (see Vol. I, pp. 69—76), *O. denti* is either the dominant species or it co-exists with a sibling species of *O. irroratus*, *O. angoniensis*. *O. irroratus* might have been displaced by *O. denti* or by *O. angoniensis* and it is now necessary to consider the situation between these two very closely related species.

Misonne points out that the fragmentary distribution of *O. irroratus* (see map, p. 565) suggests a very widespread ancient dispersal that has been broken up by "augmentation de l'aridité". This species may therefore have been dominant at one time over a great part of Africa. With an increase in aridity the resultant isolation would have offered opportunities for populations to adapt to local conditions and, in at least one locality, this may have meant some sort of adaptive adjustment to fire.

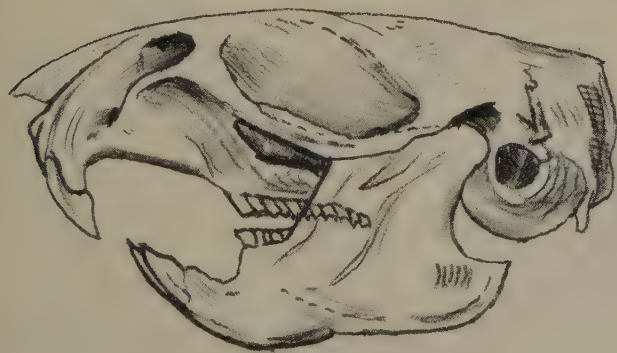
O. angoniensis appears to be just so adapted and it occurs widely within the fire-degraded vegetation belts of southern, central and eastern Africa. This species must have derived from *irroratus* but it has become genetically distinct for the two species are sympatric in parts of Kenya.

Otomys anchietae could possibly occupy a somewhat similar position in relation to *O. denti* as *angoniensis* does to *irroratus*; certainly these two species are also closely related.

That ecological limitations can be the product of competition between species as well as physical conditions is suggested by the distribution of *O. typus*. This is the only species found in Ethiopia, where it occurs in alpine and sub-alpine grasslands and also below the montane forest in savannas at altitudes of 1,800—2,500 m. In East Africa, *O. typus* only occurs in the afro-alpine zone on Ruwenzori and on Mt Elgon. (A closely related species, *O. orestes*, on alpine Mt Kenya probably derived from the same stock.) Misonne notes similarities in the distribution of *O. typus*, *Tachyoryctes* and *Lophiomys*. *O. typus* has some resemblance to *O. denti* and it is possible that the former originally differentiated through isolation in Ethiopia and later spread to the Kenya and Uganda mountains in a wet period.

Otomys are very difficult to identify and their relationships are obviously very complex. The discussion above suggests one facet of the situation, but their taxonomy is still far from clear and a great deal more work is needed on this interesting group.

Otomys irroratus.



KEY TO

<i>Species</i>	<i>Ecology and colour</i>	<i>Measurements</i>	<i>Lamellae on M₃</i>	<i>Grooves on lower incisors</i>
orestes	Alpine, Mt Kenya, dark brown	H. & B. 151—175 mm T. 65—77 mm Hf. 28—30 mm	7—8	1
typus	Montane and alpine, dark brown	H. & B. 132—175 mm T. 64—105 mm Hf. 21—30 mm	5—8	2
denti	Secondary growth, very dark all over	H. & B. 150—170 mm T. 96—95 mm Hf. 26—27 mm	5—6	1
anchietae	Uplands, dark brown	H. & B. 175—217 mm T. 87—127 mm Hf. 36—41 mm	5—8	1
angoniensis	Southern savannas, grey	H. & B. 160—209 mm T. 80—120 mm Hf. 25—35 mm	7	1 $\frac{1}{2}$
irroratus (includes tropicalis)	Dense scrub and grassland, grey to brown	H. & B. 124—216 mm T. 69—112 mm Hf. 27—34 mm	6—8	1 $\frac{1}{2}$

OTOMYS



Otomys typus
Otomys orestes
 (Mt Kenya only)



Otomys anchietae
 (horizontal)
Otomys denti
 (black)



Otomys irroratus
 (horizontal)
Otomys angoniensis
 (vertical)



Otomys orestes

**Groove-toothed
Rats, Otomys Rats
(Otomys)**

**Family
Order
Local names**

Cricetidae
Rodentia

Gudi (Kihehe), Nuke (Kikinga),
Sogo (Kinyika), Mbewa
(Kinyakyusa), Mbole (Lugisu),
Irole (Luhya), Murusti (Sebei),
Mburustit (Masai), Kitwamusanzi
(Lukonjo), Kihukuzi (Lutoro)

Groove-toothed Rats, *Otomys* Rats (*Otomys*)

Otomys are easily identified by their dark shaggy fur, stout limbs and short tail and by the grooving of both upper and lower teeth.

The special ecological role of *Otomys* has been discussed and comparisons were made with the Holarctic voles.

Within the genus the variety of habitats occupied by species may influence their choice of nest sites, some building nests of fine grass at the bottom of simple burrows dug in soft soil, others nesting at the base of a clump, while others appear not to make nests. It is not clear whether these differences are a response to local conditions or whether they are characteristics of species.

Otomys are almost exclusively herbivorous, eating green grass, reed and herb stems, shoots, bark and occasionally roots, seeds and berries. Verheyen and Verschuren (1966) noted one instance of ants being eaten. The rats have favourite feeding areas, where they cut up stems into short pieces, stripping away any hard outer layers and eating the pith. Little piles of these pieces can be found lying in the feeding places and in the runs of *Otomys*.

Otomys probably depend most on hearing to escape enemies and on sound to communicate with one another, although scent is also important. They can be heard to squeak and Lang heard them make a loud screeching noise that resembled a squirrel's call (Hill and Carter, 1941). In captivity they are very sensitive to noise, judging by the twitching of their ears and their jumps. They are very timid and meek in disposition and Verschuren found captive *O. irroratus* killed and eaten by smaller species of rodents with which they had been confined.

They seem to be most active around dawn and dusk, but like most herbivores they probably spend long hours feeding. I found four *O. irroratus* and three *O. denti* skulls in a cache of some sixty owl pellets (*Tyto capensis*). Trapping too shows that *Otomys* are about both by day and by night.

Augur buzzards (*Buteo rufofuscus*) are a major predator and *Otomys* remains are common in their pellets. The rats are naturally most vulnerable to aerial predators in more exposed vegetation.

Otomys are able to swim and during the rains the habitat of some species is often flooded, so that much of their time must be spent in the water. Nonetheless they are not primarily aquatic animals.

In South Africa, *O. irroratus* have been found to have a range of about 300 m and marked individuals were never found outside a total area of about 20 hectares. Their social structure seems not to have been investigated; Dieterlen (1968) thinks that they are not social animals, Ansell (1960a) calls them semi-communal, while Vesey-FitzGerald (1966) speaks of them as living in small colonies. Misonne has investigated the relative density of *O. irroratus* in four habitats in the Haut Ituri district of the eastern Congo (Zaire) and he has also compared the relative proportions of species. There is an appreciable drop in the numbers of *Otomys* living in savanna away from the villages, where the grass is more prone to fire and there is less secondary herbaceous growth.

Grass savanna away from villages	Savanna with secondary growth near villages	Herbaceous growth bordering marsh	Marsh
23.3 p.h.	42.5 p.h.	31.7 p.h.	16.1 p.h.
36.9%	38.8%	24.4%	17.3%

(The percentages are of total rodents and insectivores present.)

As habitats become drier still, the herbivorous niche is taken over by *Tatera* and *Arvicanthis*, which escape the increased exposure by living in burrows.

What is known of the ecological and geographic separation of species is indicated in the graphic key to *Otomys* and there was some discussion of this earlier. The nature of one species' dominance over another in particular habitats is an interesting field for enquiry.

Otomys do not, normally, attack crops at all but *O. irroratus* have done extensive damage to forest nurseries in South Africa. In Zaire (Congo) Dieterlen (1966a) estimated that 65% of the trees in one plantation had been damaged by *Otomys*; in many cases trees of 3—15 cm diameter had been completely ring-barked and died afterwards.

Otomys denti have damaged cypress trees in Kenya and Uganda, eating the bark and cambium of young trees of 1—8 years old; most damage occurs on trees 40—150 mm in diameter. The gnawing is in patches round the butt and the main damage is in plantations with luxuriant undergrowth.

Since *Otomys* do not take bait readily, trapping and poisoning are not very effective methods of control. Furthermore, poisoning kills natural predators and may even aggravate the problem. Whiteley (1969) reports that removal of grass and herb cover together with pruning of the trees up to five feet is the best and surest method. This exposes the rodents to attack by natural predators and removes perches for the animals to climb up the trunk. The same author reports a large scale fluctuation in the size of *Otomys* and *Lophuromys* populations in Kigezi. Great numbers of these animals died suddenly at Muko Forest Reserve in 1949 following three years of high density. Large fluctuations had not previously been recorded for these genera but are well known for other rats. The Forest Department organized a trapping and poisoning programme in 200 hectares of Mafuga softwood plantation in 1952; together with organized drives 12,826 rats, mainly *Otomys* and *Lophuromys* were killed. Misonne's optimum density for *O. irroratus* is 42.5 per hectare, for *Lophuromys flavopunctatus* 18.9 per hectare. The total of 61.4 rats per hectare comes remarkably close to the Mafuga figure of approximately 64 rats per hectare. In the same year (1952) 17,000 rats were destroyed by cultivators in Ndorwa and Rukiga, and the local authorities in Kigezi district reported trapping 178,305 rats in 1955. The biomass of *Otomys* in an optimum habitat can therefore be calculated at about 5½ kg per hectare and the importance of this species can be appreciated. Even higher densities than this have been recorded and Dieterlen (1966b) has estimated 357 rodents

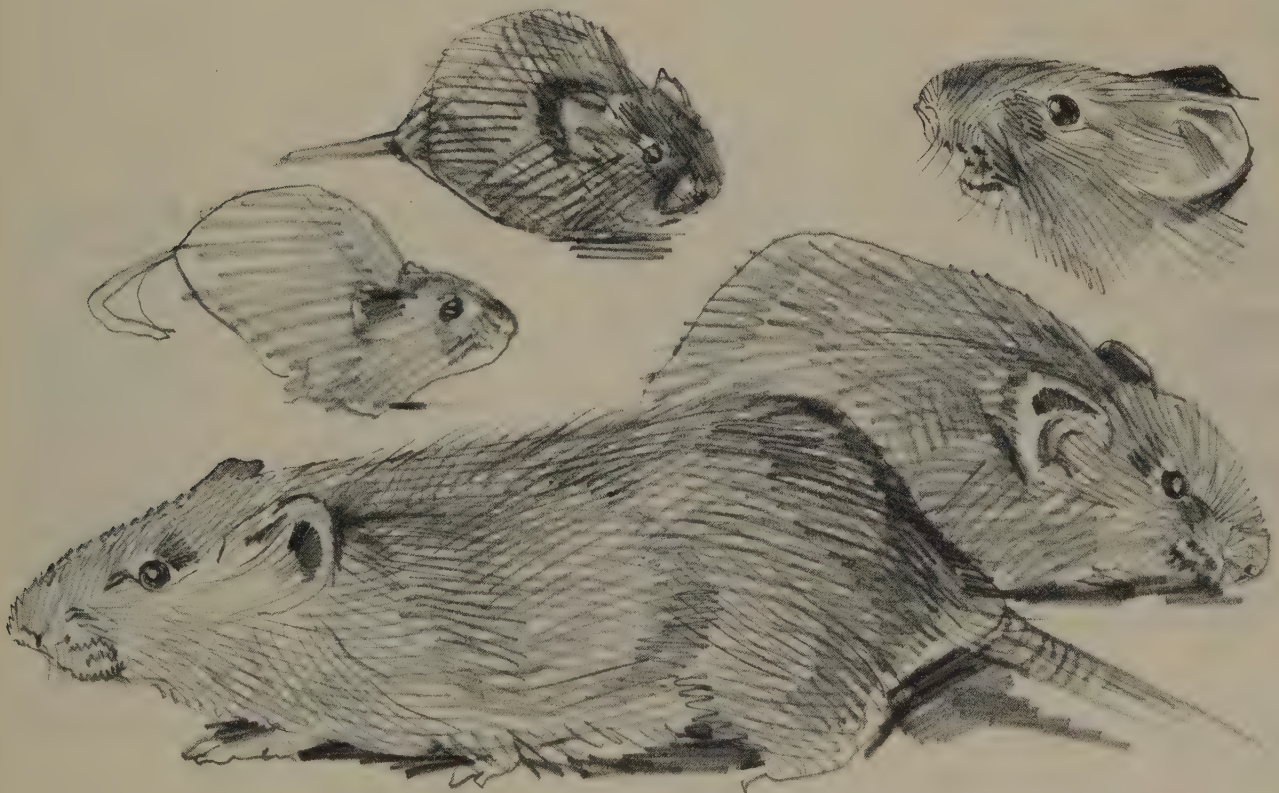
per hectare in the neighbouring Lake Kivu district, which gives a total rodent biomass of about 10 kg per hectare.

Dieterlen has implicated *Otomys* as a plague reservoir, but there is probably little direct contact with man and its role as an immediate transmitter of the disease must be very slight.

Otomys are known to have not more than 4 young and usually only have one or two at a time. This very low reproductive rate may be balanced out to some extent by more or less continuous breeding, for there is no evidence of a breeding season. The young are born with their eyes open and are well haired and able to run at birth. I have snap-trapped a female *O. irroratus* which had its young one lying dead beside it, untouched and with no sign of damage.

Capable of breeding before it is 3 months old, *Otomys* can have up to 5 litters a year. All features of adult behaviour are present before the age of 2 weeks. Average weight at birth is 12.5 g and rats gain nearly 10 g a week. Average adult weight is 150 (100—200) g.

That *Otomys* are anti-social has been shown in a recent study of the behaviour of *O. irroratus* by Davis (1972) who observed marking with the anal glands and well-developed threat displays. An aggressive rat approaches a conspecific slowly with the body low and the tail shivering. Sometimes an attack is preceded by a sideways turn presenting the animal's profile. Submissive animals instead rear up on their hindlegs and may even fall over as they present their vulnerable belly. This appears to inhibit further attack whereas flight excites pursuit and severe rump biting.



Rats and Mice

Muridae

The murids are not easily distinguished from other rat-like rodents and an examination of the structure of the molar teeth is sometimes the only certain means of identifying them as murids. Drawings of an upper tooth row have therefore been included to illustrate each genus. These are from young animals with minimal tooth-wear.

Considering the "lumping" that is done in other groups, it is easy to complain about the number of murid genera and suggestions have sometimes been made as to how the number could be cut down. For instance, *Mylomys*, *Pelomys*, *Lemniscomys* and *Rhabdomys* are all rather close. Lumping here might clarify some relationships, but at the same time it might obscure some refinements in their ecological differentiation. Besides, these genera have well-established names and are, for the most part, recognizable entities.

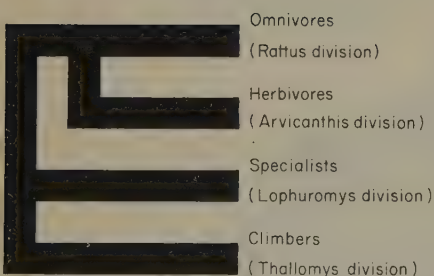
The murids provide an interesting spectacle of evolutionary radiation. Because they are of relatively recent origin they have not yet filled all possible niches and their predecessors, the cricetids, are still holding on in some areas and may be pre-eminent in some specialized niches and even incontestable in others—i.e. Dendromurines and Gerbils.

The living murid species themselves are at different evolutionary levels; some are clearly dominant species, which may be actually replacing earlier forms, while others appear to be older types that have entered a peculiar niche and started to specialize. Evolution in African murids has not proceeded as far as it has in their Indo-Australian homeland. Even an aberrant form like *Colomys* still has a strong "family likeness" and it has not adapted to its aquatic existence to anything like the same degree as the various Indo-Australian water rats like *Hydromys*.^{*} The evolution of this species provides a most interesting topic, which will be discussed shortly, but the broad trends in the murid radiation should be outlined first.

The murids probably entered Africa some time in the early Pliocene, for they are unknown in the African Miocene and had already differentiated in the Pleistocene. Some idea of what the oldest stock of African murids was like is provided by the acacia rat, *Thallomys*. The teeth of this animal are almost indistinguishable from those of *Parapodemus*, a fossil murid known from the European Miocene (Misonne, 1969). In common with *Praomys* and *Aethomys*, *Thallomys* has sometimes been treated as a subgenus of *Rattus*.

The *Rattus*-like murids represent the African branch of an ancient line that has maintained a generalized type of body form. Apart from an improvement in their occlusion, the teeth have kept a primitive arrangement and these rats seem to have "specialized in being unspecialized". Replacement of one closely related species by another is probably continuous and in this way the genotype is constantly being refined, but no major departure is made from what appears to be an established prototype for rodent success.

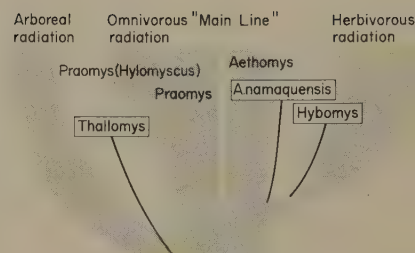
^{*} *Leptomys* from New Guinea is a remarkably similar equivalent species.



The acacia rat, *Thallomys* links what Misonne calls the "Rattus division" with a group of rats that have become arboreal; this group of climbers includes *Thamnomys* and *Oenomys*. All the species of the latter group have a relatively primitive tooth structure and, but for their adoption of a special niche, could be described as relic species. The forest forms, *Thamnomys venustus* and *T. rutilans* in particular, may be giving way before an arboreal offshoot of the *Rattus* division, *Praomys* (*Hylomyscus*).

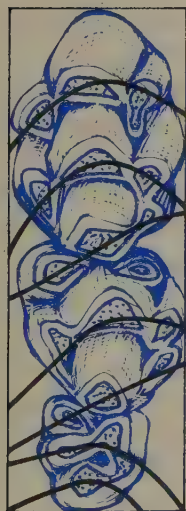
The *Rattus* division also includes the interesting genus *Aethomys*. One species, *A. namaquensis*, links what Misonne (1969) calls the "main line" of murid evolution with a special African radiation of herbivorous murids, which Misonne calls the "*Arvicanthis* division". The genus most like *Aethomys namaquensis* is *Hybomys*. It is conceivable that this genus represents the modified relics of a formerly dominant type which has been completely eliminated outside the forest. Within the forest it is locally distributed but is very numerous where conditions are right for it. Another herbivorous species, resembling *Aethomys*, is the swamp-loving species, *Dasymys*, but the main herbivorous line clearly derives from a *Hybomys* type and there is a more or less steady progression in the molar dentition towards greater strength and breadth. This progression can be illustrated by comparing the teeth of *Hybomys*, *Rhabdomys*, *Lemniscomys*, *Pelomys* and *Arvicanthis*.

The remaining murids are species that have tended to adopt an insectivorous diet and of all the African groups have modified their body-form and habits the most. Of these perhaps the closest to the main line is *Zelotomys*, which looks rather like *Praomys* externally. *Lophuromys* may also have derived from a similar form and the genus *Uranomys* must also share the same ancestry. *Acomys* seems to have evolved out of a *Uranomys*-like stock.

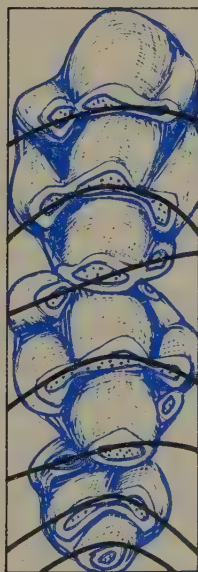


Hypothetical relationships of linking forms *Thallomys* and *Aethomys namaquensis* to the arboreal and herbivorous murid radiations.

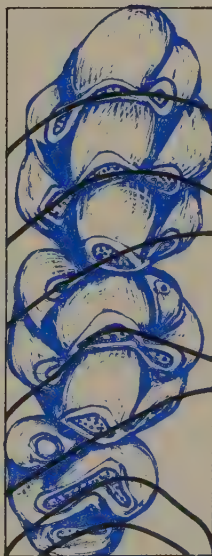
Tooththrow patterns for 5 herbivorous murids showing asymmetric cusps of more primitive forms and symmetrical lamellae-like arrangement in the most advanced form *Arvicanthis*.



Hybomys.



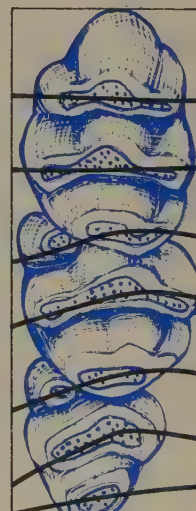
Rhabdomys.



Lemniscomys.



Pelomys.



Arvicanthis.

The other specialized radiation from the same stock as *Zelotomys* and *Lophuromys* is that of the swamp forest rats, *Colomys* and *Malacomys*. These swamp-forest species illustrate the role of climatic change in the evolution of African forest mammals and they also provide an interesting example of unequal evolutionary development. *Malacomys* has the more highly modified teeth and the less extreme body build; *Colomys* has adapted further to aquatic life while the tooth structure is more conservative. A correlation between the forms of this murid complex and the main Forest Refuges was presented in Volume I, and I conveyed the erroneous impression that *Colomys* was altogether more advanced than *Malacomys*. In point of fact, the retention of a more rat-like form by *Malacomys* may be the reason for its greater success. (We have here semantic problems since the use of words such as "success", "advanced", "conservative", "specialized" must be qualified at every turn as they can apply to one facet of the animal's evolution and not to another.)

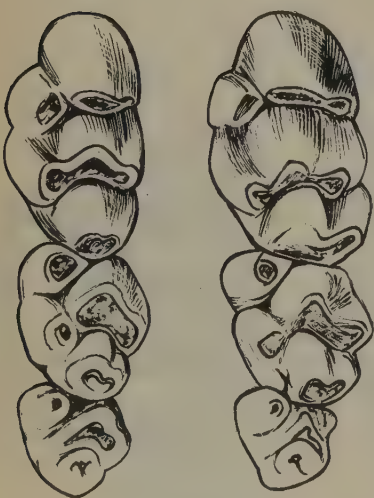
Central to the discussion of these rodents is the West African *Malacomys cansdalei*. In describing it, Ansell (1958) noted that it was a very distinct form and pointed out that the relationships of *Malacomys* had better be "left *sub judice* until more material is available and in particular until it can be determined whether *edwardsi* and *cansdalei* are really allopatric or not". Since that time D. H. Barry (in Rosevear, 1969) has established that these two forms of *Malacomys* co-exist in the Ankasa Forest Reserve in Ghana. If we follow Heim de Balsac and Lamotte (1958), who regard *edwardsi* as a race of *longipes*, it becomes necessary to regard *cansdalei* as a distinct species of *Malacomys*. There are further reasons for regarding it as distinct which will emerge in the following discussion.

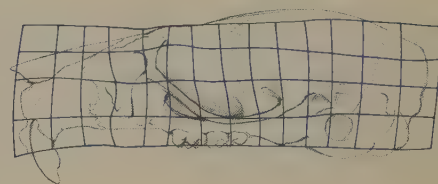
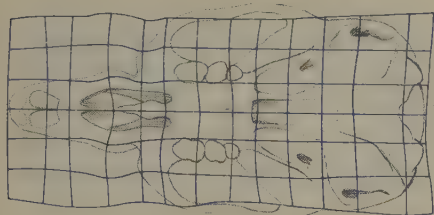
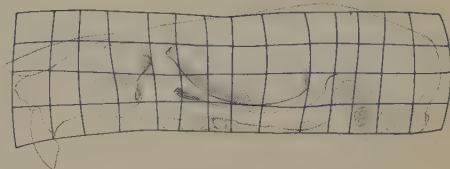
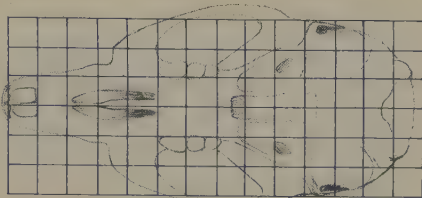
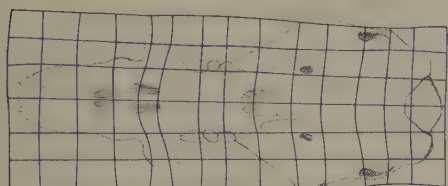
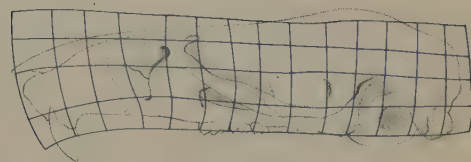
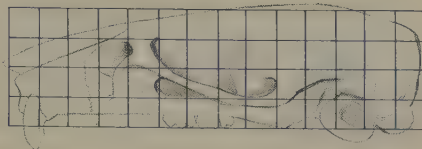
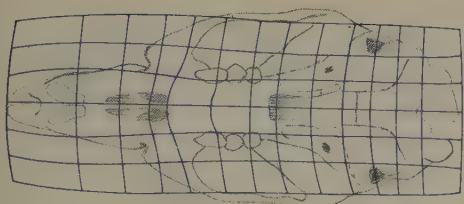
Malacomys cansdalei is of special interest here because it gives some indication of the common origins of *Malacomys* and *Colomys*. In this form the general elongation of the skull, which is so typical of the genus, has not proceeded so far as in *longipes*, nor have the molars narrowed to the same degree. (It is conceivable that this last trend in *Malacomys* is simply a necessary accommodation of the teeth to the overall narrowing of the skull and that as their anchorage narrowed a better interlocking between the individual teeth was achieved.)

This narrowing may be contrasted with the relatively broad, sharply cusped teeth and bulbous cranium of *Colomys*, peculiarities that are probably linked. The typical rodent adaptation to hard diets has required well-developed muscles as well as reinforced skull architecture with strong grinding teeth. *Colomys* has entered a niche where it is able to feed very largely on soft foods, worms, slugs and perhaps soft plant material. This seems to have resulted in the loss of the temporal ridges and an extreme narrowing of the zygomatic arch and its associated plate and process, which have contracted longitudinally. This functional decline has led the premaxilla to move back slightly, causing the maxilla to buckle out on either side of the incisive foramen. The backward movement is also betrayed by the dragging back of the suture between the maxilla and premaxilla at the point where it runs over the incisor root and by the contraction of the frontal-nasal joint.

These peculiarities, which I interpret as a secondary contraction of the muzzle after an initial lengthening in an ancestral form, can be illustrated by means of a co-ordinate system similar to that used to compare Cercopithecoid

Left upper molars of *Malacomys* (left) and *Colomys* (right).





Malacomys longipes.

hypothetical
ancestor.

Malacomys longipes.

Malacomys cansdalei.

Malacomys cansdalei.

Colomys goslingi.

Colomys goslingi.

skulls in Volume I. To achieve figurations that emphasize the different trends of the two genera, a symmetrical co-ordinate should be imposed upon a non-specialized model. In this case, this hypothetical skull is constructed from an amalgam of the species with some common features borrowed from *Thallomys*, *Lophuromys* and *Zelotomys*. In some respects *M. cansdalei* has the least peculiar skull but has a somewhat extended muzzle, a feature which is very much more extreme in *M. longipes*. The allometry that is associated with the smaller measurements of *Colomys* may influence the relative size of its cranium as much as the reduction in musculature. However, the important point is that the co-ordinates illustrate the disturbance that has taken place between the main body of the skull and the muzzle. This secondary reduction of the nose may be related to the peculiar hunting technique of this rat and the development of a "closed mouth" instead of an "open mouth" like *Malacomys* (see overleaf).

If we consider the zoogeography of the group, the over-simplified table in Volume I, which lists five forms in three refuges, can be extended to include all known forms, which involves eight species and/or races centred on five refuge areas. Taking into account their morphology and assuming that the mechanism for their evolution has been provided by climatic fluctuations, we

Silhouette of fleshy parts in relation to the skull in *Colomys* (left) and *Malacomys* (right).



can explain their present-day distribution in several ways. Below there is a simplified diagrammatic reconstruction of the possible history of the group. It starts with a common ancestral stock (dotted texture) splitting into two populations. The distribution of *Colomys* on the eastern side of the continent is very far-flung while that of *Malacomys* is essentially West African. Of the living swamp-forest rats *Colomys* is probably the "oldest"; however, the common ancestral stock must have occupied a less well-defined niche than either of the contemporary genera; although this niche must have been closer to that of *Malacomys*.

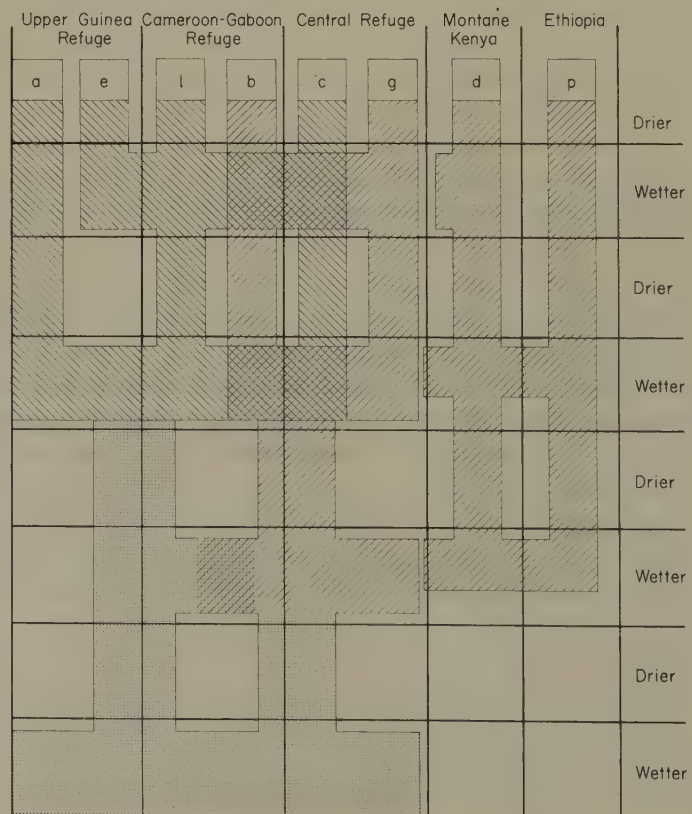
The original stock having been physically separated by a dry corridor and genetic differences having arisen, a later joining up of the forests may have allowed the two populations to meet up again, and it is probable that this

Diagram showing role of forest refuges in the hypothetical differentiation of the *Malacomys-Colomys* group.

Malacomys group a. *cansdalei*.
 e. *edwardsi*.
 l. *longipes*.
 c. *centralis*.

Colomys group b. *bicolor*.
 g. *goslingi*.
 d. *denti*.
 p. *plumbeus*.

Spotted texture: common ancestral stock.



encounter led to the eastern stock being pushed "further into the water", since it seems unlikely that the less specialized niche would be voluntarily vacated. In this way a more aquatic type emerged as the *Colomys* lineage. This encounter is symbolized in the diagram by the overlapping area of dots (the ancestral form), and diagonal hatching (*Colomys*).

It is, of course, uncertain where this encounter might have taken place but the Cameroon-Gaboon Refuge is the most likely site. (Subsequent to this encounter, both stocks probably continued as sympatric species but, as a matter of graphic convenience, I have represented them in the diagram as separating again). After this primary differentiation the genus *Malacomys* probably emerged in a recognizably modern form, and I suggest that *Malacomys cansdalei* represents this stock in a little-changed condition. The absence of *Colomys* in this area might have allowed this type to fill both swamp rat niches until the later arrival of *edwardsi*. Where *Colomys* and *Malacomys* co-existed their separate ecological roles may have become more exactly defined through mutual interaction, and the presence of *Colomys* may have been as much a factor in the "moulding" of *Malacomys* as vice versa. This interaction may have been continuous over a long period in both the Cameroon-Gaboon and Central Refuges.

M. l. longipes and *M. l. centralis* are most alike and their similarity is clearly due to a greater measure of gene-flow. It may also be encouraged by ecological constraints through competition from *Colomys* (and possibly also from *Deomys*). In the Upper Guinea Refuge where both these competitors are absent, Cole (in Delany, 1972) has found that *cansdalei* and *edwardsi* share a very similar diet of slugs, earthworms and plants but the former is more frequently trapped in the lower wetter valleys whereas *edwardsi* is caught on the higher, drier ground. At what stage *Colomys* managed to invade Kenya and Ethiopia is open to question but the species' ecological role in these areas where there are no competitors might be quite different.

I have dwelt on the radiation of these species at some length, partly because I have had the opportunity to study them in more detail than many other species, but also in order to illustrate what a fertile field for enquiry is provided by the African murids.

In the profiles of species I have touched on competition between species but a great deal of background work needs to be done, and anyone with time on their hands and a few traps can gather very valuable data by noting the numerical abundance and the condition of species caught, carefully recording details of the locality, the habitats, the season and so on. The study of whole rodent communities and the interaction of species has scarcely begun but it holds much promise. Even the broadest outline of murid ecology in Africa would present a very complex picture and it will not be attempted here.

The broad diversification of African murids into climbers, omnivores, herbivores and insectivorous forms allows each habitat to support a different spectrum of murids and members of each group can generally be found in each major vegetation type. A list of species by vegetation zones is given on p. 366. Catalogues of some rodent associations are available in Misonne (1963) and in Delany (1972).

Diversification of niches can be achieved in many ways, one of which is the separation of activity periods in species using similar resources in the

same habitat (an example of nocturnal-diurnal separation between two species of murids was given in Volume I).

The behaviour of rodents, particularly of laboratory rats and mice, has been the subject of thousands of papers, so a generalized account of murid behaviour is rather pointless; however, in the profiles that follow data on behaviour as well as on their potential as laboratory animals are also mentioned.

Few murids have a productive life of more than 9 to 18 months but their fecundity is legendary and there can be little doubt that they support the majority of carnivorous animals—including many felines and canines.

The destructiveness of particular species in relation to food crops and forestry is discussed in the following profiles and the role of *Rattus* and *Praomys* in the transmission of plague and other diseases is also outlined in the profiles of the species.

I hope the following accounts will help to identify some of the areas of ignorance and encourage others to investigate some of the numerous problems that murids pose.

Many murid rodents communicate with ultrasound. Sewell (1967) has shown that the young of most species use it; many employ it in the course of mating; some make ultrasonic signals while fighting, threatening or in submission and the lactating females of some species also appear to communicate with their young in this way.

GENERIC KEY TO THE "OMNIVORES" OR *RATTUS* AND *MUS* DIVISIONS

- | | | |
|--|----------------------------|----------|
| 1. Medium size (H and B 100—250)
Small size (H and B 50—100) | ²
<i>Mus</i> | (p. 600) |
| 2. Very soft short fur, clear demarkation between flanks and light belly, more delicately built | <i>Praomys</i> | (p. 583) |
| Longish fur, yellowish or greyish brown with a metallic sheen | <i>Aethomys</i> | (p. 595) |
| Coarse fur, gradual transition between dark back and lighter belly, more heavily built (mostly in or near buildings) | <i>Rattus</i> | (p. 578) |
| White tail, projecting incisors (a linking form with the "specialists") | <i>Zelotomys</i> | (p. 659) |
-



Young *Rattus rattus*.

Measurements head and body

170 (100—220) mm

tail 175 (140—230) mm

weight 150 (50—200) g

Rattus rattus

head and body

233 (200—260) mm

tail 195 (160—230) mm

weight 250—450 g

Rattus norvegicus

Local names

Panya (Kiswahili), Mbeba (many local languages), Emmese (Luganda), Oyo, Obaa (Lwo), Nkule (Kimakonde), Miri (Karamojong), Sohina (Ateso), Lutere (Lukonjo), Ngoswe (Kihehe, Kiyao, Kisambaa), Huni (Kuumba), Ewena (Lubwizi), Mabaja (Lugisu), Mabageet (Kimasai), Mairandet (Sebei), Lichunga (Luhya)

Rat (*Rattus*)

Species

Rattus rattus (black rat): nearly all villages and towns

Rattus norvegicus (brown rat): larger coastal ports

Both species of rats are relatively recent arrivals and the black rats' impact in Uganda is not easily forgotten for 60,000 people died of plague between 1917 and 1942. Although plague carried by *Praomys natalensis* had been known before the black rats' invasion, the epidemic in the twenties and thirties was of unprecedented severity.

These rats probably came to East Africa from a variety of countries and there are several distinct strains or subspecies present.

1. *R. r. rattus* : Blackish back, grey belly (Europe?)
2. *R. r. frugivorus* : Brown back, cream belly (North India)
3. *R. r. alexandrinus* : Brown back, grey belly (Middle East?)
4. *R. r. wroughtoni* : Rufous back, white belly (South India)
5. *R. r. kijabius* : probably hybrid of 1 and 3 (East Africa)
6. *R. r. rufescens* : Rufous back, grey belly (West India)

Rattus norvegicus : Brown, large (Europe)

The segregation of sympatric races is a very rare phenomenon, yet Feldman (1926) found mixed populations tending to maintain their identity. When crosses were made in the laboratory he found that *R. r. rattus* was genetically dominant over *R. r. frugivorus* and that this in turn was dominant over *R. r. alexandrinus*.

Misonne (1969) also reports two Javanese forms, *R. r. diardi* and *R. r. breviceaudatus*, living side by side, one in the villages and fields, the other only in the fields. The two forms do not seem to interbreed in spite of having the same chromosome structure and number.

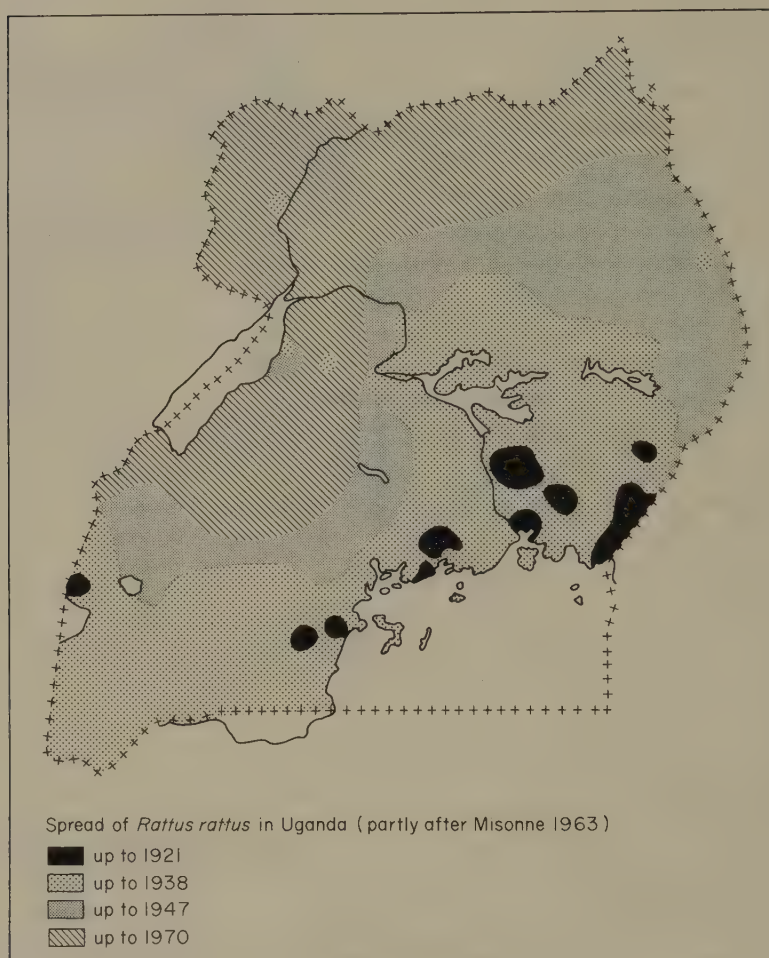
The map below shows the distribution of some *Rattus* subspecies in Tanzania (from Swynnerton and Hayman, 1951). The map overleaf shows the spread of *Rattus rattus* in Uganda (after Baker, 1922, Misonne, 1963 and Prentice, personal communication).

The biology of rats has been the subject of countless publications. There are, for instance, well over 2,000 works on the behaviour of *Rattus rattus* alone. One good recent text is Barnett's "A Study in Behaviour" (1963).

Although associated exclusively with man-made structures, houses and stores at the present time, it is always possible that a "wild" form could arise to carry the *Rattus* invasion still further into the African countryside.



Nests tend to be made in different spots according to the species; *R. rattus* in the roof and *R. norvegicus* in burrows underground. Any handy material may be used.



Rats will eat all types of human foodstuff and much else besides including soap, hides, paper and beeswax. Rats are dependent on water or at the very least moist foods. They sometimes hoard food and often carry items back to the nest to eat. Both species are nocturnal. The principal distinction between the species in activity is that *R. rattus* is more of a climber, *R. norvegicus* more of a digger and swimmer.

Populations have been observed to fluctuate over long periods in various parts of the world and Harris (in Hopkins M/S) has observed a regular decline in numbers in Tanzania towards the end of the rains and a rise of numbers after the grain harvest, when there is a reproductive peak. The density of rat infestation also varies greatly and during the worst period of plague in Uganda, 35 rats could be found in the thatch of one hut. Baker notes that in 1921 plague-infected rats were always *Rattus rattus*.

"In the plague area at Kamuli in 1921, about 99% of the rats killed in the thatch of huts were of this species, which the natives stated had been unknown to them five years previously, and whose introduction they attributed to the erection of ginneries. He notes that 'within a mile or so of the cotton ginneries the houses contained twice as many rats as elsewhere'. At the periphery of the plague area rats were less plentiful in huts and consisted of *R. rattus* and *R. coucha* (*Praomys natalensis*) in about equal numbers, while outside the area *R. rattus* did not occur. His observation with regard to the greater abundance of rats near the ginneries is not borne out by work by Hopkins (1938), nor does his work support the inference that ginneries have some special connection with *R. rattus* and with plague, but if ginneries are regarded merely as centres of immigrant population a probable explanation of Baker's facts is that his belief that the species was newly introduced and had not yet had time to spread far is correct". (Hopkins M/S.)

There can be no doubt that *R. rattus* is the principal vector of human plague, even though many indigenous African rodents and also hares can act as reservoirs in areas where the disease is endemic. In southern Africa a chain of transmission has been observed starting with *Tatera* to *Praomys natalensis* to *Rattus* to *Homo*. In Kenya, Heisch *et al.* (1953) have shown that wild rodents are infected.

The margin map shows the distribution of plague outbreaks in Africa between 1899 and 1949 (after Davis, 1953). Roberts (1935) described plague as flourishing best in warm wet weather after a peak in rat numbers; such conditions favour the plague flea, *Xenopsylla brasiliensis*, whereas dry weather reduces their numbers. Hopkins (1949) notes that the endemic areas in Africa are all within the 1,150 mm rainfall area.

The East African ports are free of plague and *R. norvegicus* is not implicated in plague transmission. It is, however, an agent for human leptospiral jaundice and trichinosis and contaminates foodstuffs with *Salmonella*, which is responsible for food poisoning.

Rats are extremely difficult to control. Once familiar with traps and poisoned bait they become extremely wary of them.

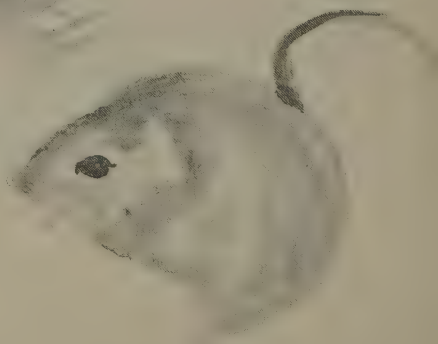
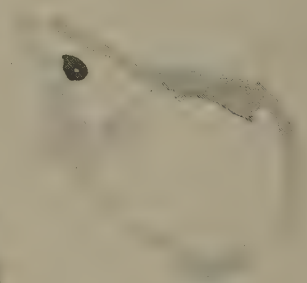
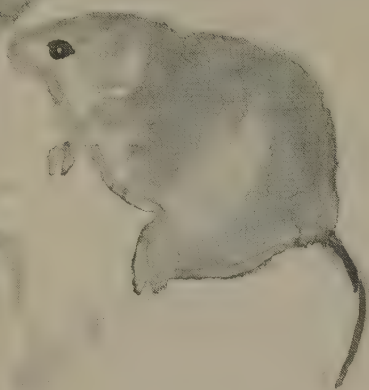
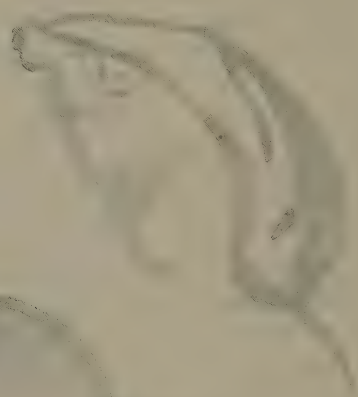
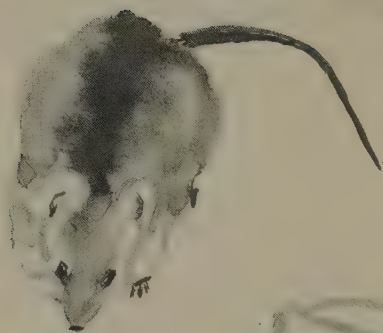
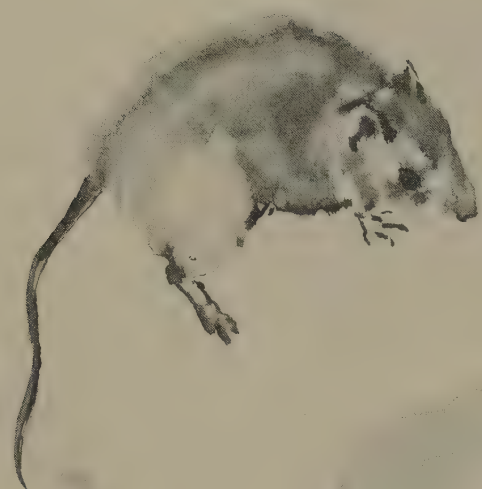
All rats use habitual paths, even in open rooms, and unbaited traps set along pathways may be more successful than baited ones. These pathways are often betrayed at corners, etc. by greasy smears, but a sprinkling of fine white powder will most clearly reveal their routes. Cats are probably the best means of keeping numbers down and may even stop re-invasion after rats have been eliminated; however, they have proved unable to actually eliminate rats in the first place. Wild predators are numerous and include many species of carnivora, birds of prey and snakes.

Correlations between breeding peaks and crop harvests have been mentioned and there is experimental evidence that nutritional levels influence the numbers of young and the number of litters.

Oestrus is very short and recurs every ten days. Gestation is 21—30 days in both species. There is post-partum oestrus allowing continuous breeding. The number of young averages 6 or 7 but very occasionally reaches 17. They are born blind and naked and grow rapidly. *R. rattus* are sexually mature at 3—4 months, by which time they may weigh 70—140 g. The turnover of population is very rapid and very few wild rats live more than one year.



Distribution of plague outbreaks in Africa.



African Soft-furred Rats (*Praomys*)

Subgenera

P. Myomyscus

P. Mastomys

P. Praomys

P. Hylomyscus

For many years this genus has been treated as one of the African branches of the world-wide genus *Rattus*. On anatomical grounds this treatment is difficult to quarrel with for the genus is a typical omnivorous generalized group of rats. However, Misonne (1969) has stressed that it is important to recognize this as a distinct African line belonging to a conservative but also extremely successful division of murids, which runs parallel to the true *Rattus*, which is originally an Oriental genus. A detailed study of tooth structure shows that *Praomys* has close affinities with African murids that cannot be classified with *Rattus*. Furthermore, numerous African murid genera are of very recent formation, while the origins of *Rattus*-like forms probably go back at least to the early Pliocene.

Of the *Praomys* radiation as a whole Misonne thinks that *P. (Myomyscus)* might be the more ancient. If this is correct, it illustrates that within any evolutionary radiation relatively unmodified descendants of older forms can be successful or at least survive, even if they no longer occupy the choicest habitats.

Misonne also tentatively suggests that *P. (Hylomyscus)* might be the most advanced member of the group. It should be pointed out, however, that *P. (Hylomyscus)* also represents a departure from the generalized niche occupied by most *Praomys* species. Although there has been a slightly divergent radiation within the other *Praomys* subgenera, none have entered into an entirely new milieu but *P. (Hylomyscus)* has definitely adapted to an arboreal way of life.

The presence of *P. (Praomys) delectorum* and of *P. (Hylomyscus) denniae* in the older "Southern Forests" of Tanzania (see Volume I, p. 69) is indicative that the expansion of both these forms is relatively ancient. *P. (Hylomyscus) denniae* is, however, very close to *P. (Praomys)* and was classified as such by Ellerman *et al.* (1953). It probably represents a link between the two subgenera that has become displaced in the more choice habitats by advanced forms such as *P. (H.) stella*.

Praomys (Mastomys) natalensis seems to have a very interesting history of expansion in association with man. Rather as a local Malay population of *Rattus rattus* adapted itself to human dwellings, so *P. (M.) natalensis* accommodated itself to the African village. The only area where this species lives completely independently of man is in the southern savannas, so it is probable that its natural range was once very much more limited than it is now, when it can be found all over Africa south of the Sahara and even in Morocco. However, it is declining in many areas as the "Development rat", *Rattus rattus*, expands its range.

Teeth

KEY TO THE SPECIES



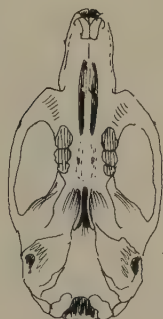
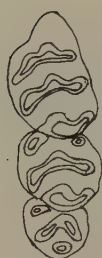
P. (Myomyscus)

1 species

P. (M.) fumatus

H. & B. 98 (75—105) mm
T. 125 (97—150) mm
Hf. 22 (20—24) mm
Wt. 30 (24—35) g

Broad molars. Species of rocky country in dry savanna.



P. (Mastomys)

2 species

P. (M.) natalensis

H. & B. 125 (90—155) mm
T. 112 (88—150) mm
Hf. 24 (18—30) mm
Wt. 48 (20—70) g

P. (M.) pernanus

H. & B. (62—77) mm
T. (52—66) mm
Hf. (14—17) mm

P. (M.) pernanus is a rare pigmy form from Lake Victoria region.

P. (M.) natalensis. Common domestic and savanna species. 17–22 mammae.



P. (Praomys)

2 (forest) species

P. (P.) delectorum

H. & B. 100 (94—125) mm
T. 123 (110—140) mm
Hf. 22 (20—25) mm
S.L. 27 (26—29) mm
Wt. 35 g

P. (P.) delectorum. Smaller species, satiny coat, 8 mammae.

AND SUBGENERA OF PRAOMYS

P. (P.) jacksoni

H. & B. 120 (100—140) mm
T. 145 (120—165) mm
Hf. 25 (22—30) mm
S.L. 31 (30—36) mm
Wt. 40 (21—57) g



Larger species, velvety coat, 6 mammae.

P. (Hylomyscus)

3 (forest) species

P. (H.) denniae

H. & B. 100 (71—120) mm
T. 125 (100—172) mm
Hf. 20 (19.5—22) mm
Wt. 20 (8—42) g



Relict species, mainly on mountains, underside buff-grey, 8 mammae.

P. (H.) aeta

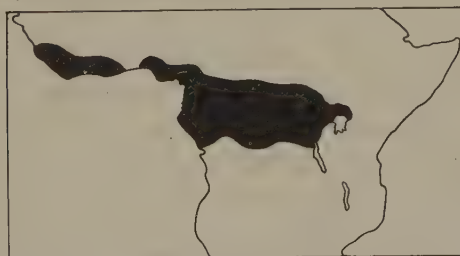
H. & B. 90 (80—107) mm
T. 135 (125—146) mm
Hf. 20 (18—21) mm
Wt. 20 g



Short, dull-coloured fur, strong ridges above eye sockets. Lowland forest species, 6 mammae.

P. (H.) stella

H. & B. 90 (79—104) mm
T. 130 (111—150) mm
Hf. 18 (16—20) mm
Wt. 18 (15—24) g



Bright colour, underside white. Forests from Guinea to Kenya, 8 mammae.

In one intensively trapped Uganda forest nearly 90% of the *P. (Hylomyscus) stella* caught were taken on branches (Delany, 1971). All *Rattus*-like murids can climb and it is significant that nearly 40% of the *P. (Praomys) jacksoni* taken in the same forest were also on branches. This particular environment is made up of very dense secondary growth so that the richest food resources are scattered through a three dimensional habitat that is only accessible to climbers. Such a situation can be found throughout the forests of Africa, at various altitudes, in clearings, valleys or along the forest edge (see the diagrams of forest profiles on pp. 27—28, Volume I). In moist forest areas, where there is little risk of severe drought, this thick secondary growth represents a huge resource. It appears to support a great many birds, insects and mammals. For rodents the potentials of this environment are probably far from being fully realized by the more highly specialized arboreal species, Sciuridae, *Thamnomys*, *Grammomys*, *Oenomys* and *Graphiurus*.

Unless they feed upon the rich invertebrate fauna of the forest floor—as do *Lophuromys*—terrestrial rodents must assume the role of dogs beneath a table, waiting for crumbs to fall from above—as *Hybomys* seem to do.

The versatile, generalized and prolific *Praomys* group has therefore taken to the branches very readily in order to exploit the riches of this habitat more effectively. The presence of some 10 or more *P. (Praomys)* and *P. (Hylomyscus)* species is some measure of their success in colonizing the African forests. It is possible that this habitat is not yet “saturated” with arboreal rodents and that this last subgenus is still in the process of evolutionary expansion.

Smoky Meadow Rat (*Praomys (Myomyscus) fumatus*)

This species is difficult to tell apart from *P. (Mastomys) natalensis* but usually has a tail that is longer than the body and whiter underparts, with the hairs white to the base in some localities. The pterygoid fossa is less narrow than in *P. (M.) natalensis*.

Misonne (1969) thinks that these rats might represent the most ancient form of *Praomys*. This is an interesting suggestion, because the *Praomys* group have radiated into a variety of niches, in each of which they are a dominant rodent. Thus *P. (M.) natalensis* occupies a domestic savanna niche, *P. (Praomys)* various forest habitats and *P. (Hylomyscus)* high altitude and arboreal forest niches.

P. (Myomyscus) species seem to occupy the least favourable habitats, and *P. (M.) fumatus* has become primarily a rock-dwelling rat, ranging over most of northeastern Africa in rather dry, scrubby country on mountains and outcrops. It has been recorded living in crevices and along ledges of cliffs.

Like all *Praomys* this is a nocturnal species and its behaviour probably resembles that of other members of the genus.

Multimammate Rats (*Praomys* (*Mastomys*))

Species

<i>Praomys</i> (<i>Mastomys</i>) <i>natalensis</i>	Common form
<i>Praomys</i> (<i>Mastomys</i>) <i>pernanus</i>	Rare pigmy form

The two species of this subgenus are easily separable by size and, because nothing specific is known about the pigmy form, this profile will concern the common multimammate rat.

The multimammate rat is a typical unspecialized rat. It has relatively narrow feet, a greyish brown back and a pale grey belly; a yellowish zone often separates the darker dorsal colouring from the light belly. The best distinguishing characteristics are the particularly silky grey-based fur, the tail shorter than the body and, in adult females, the presence of up to 12 pairs of mammae.

Multimammate rats are almost ubiquitous in Africa as they are closely associated with human activity. They do not occur much above 2,100 m in tropical East Africa and live by preference near houses, barns and cultivated fields. Until the arrival of the black rat, *Rattus rattus*, they were the typical hut rat of every African village. Even today they are still the dominant domestic rat in the more remote villages and in some areas they have acquired some sort of *modus vivendi* with *Rattus*, the latter tending to live in the roof while *P. (M.) natalensis* burrows under the floors and walls. Where it has been expelled from the houses it often persists on the outskirts of villages and in the fields, where its favourite shelter is in the chambers of disused termitaries. Where this rat is found living in savanna or forest clearings in the tropical zone, this can be taken as evidence of past human occupation. Misonne (1963) reports finding pockets of *natalensis* on village sites that had been deserted for over 20 years. He presents most interesting data to show that the proportion of *Mastomys* to other rodents in the immediate vicinity of villages rises to 8% when *Rattus* is present in the village itself, whereas it is 1.5% around villages which have so far escaped the invader and where *Mastomys* occurs in the huts. In southern Tanzania and southern Africa generally *P. (M.) natalensis* is much less circumscribed and this species becomes an important member of the rodent community in a variety of habitats.

"The multimammate mouse, *Praomys natalensis*, has been collected on the floor of forests with *Praomys jacksoni* and two of the species of *Lophuromys*, along drainage lines with *Otomys*, *Pelomys* and *Dasymys*, in flood plain grassland with *Arvicanthus*, among rocks with *Aethomys chrysophilus* and *Acomys*, in warrens of *Tatera*, and in villages and houses with *Rattus*. Its diet is as varied as its shelters. All kinds of stores are eaten, such as grain, mealie meal, dried fish, chocolate and soap. The multimammate mouse also has cannibalistic tendencies and is certainly insectivorous; because it feeds readily on adult locusts and excavates the eggs of these insects after they have been laid in the ground". (Vesey-FitzGerald, 1966.)

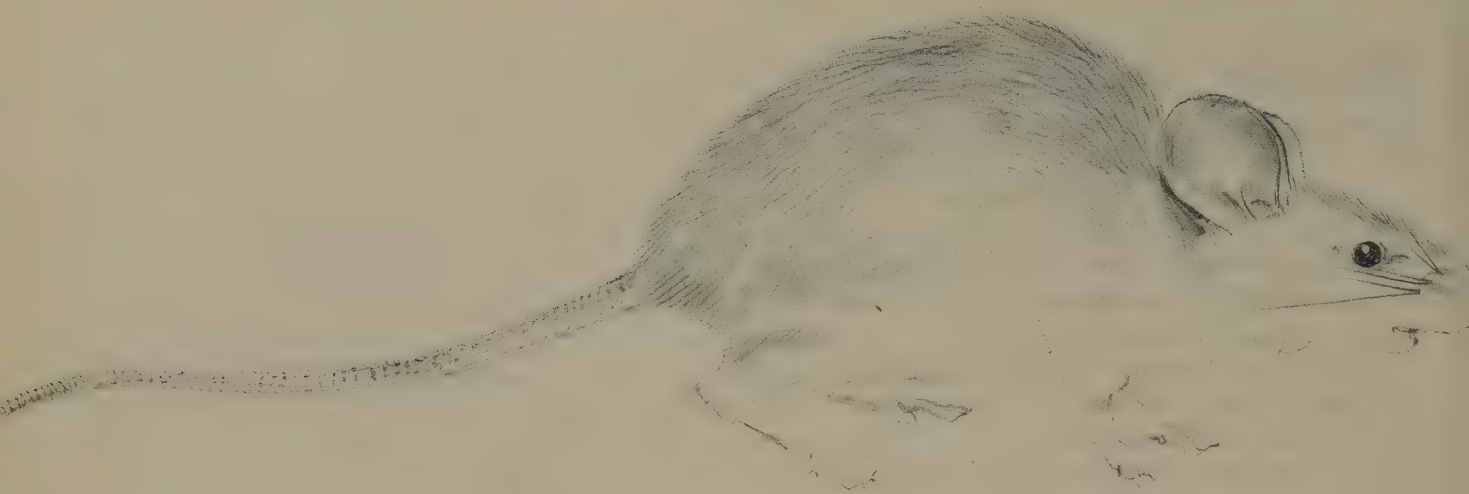
It therefore looks as though *P. (M.) natalensis* was originally an inhabitant of the southern savannas and has spread into the tropical zone as a commensal

Local names

Mese (Luganda), Ndyakiro (Lunyoro), Mvugu (Lusoga), Ikaria (Lugisu), Pwela (Kirungu), Imbewa (Kinyakyusa), Imbeba (Kikerewe), Natelewa (Karamojong), Enyzbwosi (Ateso)



Records of *P. (M.) pernanus*.



of man. Likewise, although the northern savannas are ecologically equivalent to those in the south, Misonne stresses that the status of this species is quite different in the two zones, which reinforces the suggestion of a southern origin for this species. It is found in Pleistocene deposits in South Africa and in later deposits at Tabun in Israel.

This species is extremely important because it is the principal indigenous host of human plague, the vector being its flea, *Xenopsylla cheopis*. Because it passes readily from field and bush to houses it can spread plague by acting as an intermediary between wild reservoirs and *Rattus rattus* or directly to man. Between 1928—38 nearly 20,000 people died of plague in Uganda. The severity of this epidemic may have been influenced by the profound ecological disturbance of *Rattus rattus* invading and supplanting *P. (M.) natalensis* at this time. Further discussion of plague will be found in the profile of the black rat.

The burrows of the multimammate rat are by preference modifications of natural crevices and cracks but it can dig its own burrow when forced to; they tend to have several entrances and the nest is built underground.

The diet is omnivorous and this rat is probably an opportunistic feeder like *Rattus*. In rich habitats it tends to feed as much on animal matter, mostly insects, as on vegetable matter. Where its choice is restricted it accommodates itself to feed almost exclusively on a single item, such as cassava, maize or rice. In activity cages, about 8% of their time is spent eating (Delany and Kanseriimuhanga, 1970). They are able to live in relatively dry habitats but like to drink, and they will expose themselves more than most other rodents in their search for food and water. This lack of caution must play a part in the enormous fluctuations that are typical of this species, for when these rodents are numerous various predators, snakes, owls and carnivores can glut themselves with ease.

Hordes of these rodents are an awe-inspiring spectacle; scores of them can be seen at any one time and a walk or drive along a pathway will reveal many hundreds as they twitter and scurry about, even running between one's legs. When they are killed with sticks or stones, their fellows are not affected and in villages invaded by these hordes the villagers generally become re-

signed to the rats because their numbers appear so infinite. I have seen a genet, *Genetta tigrina*, and small flocks of the marsh owl, *Asio capensis*, feeding on these rats while others ran about in the open within a few metres. Such very large numbers of *natalensis* have been recorded in parts of the Rukwa Valley in 1936, 1951, 1955, 1971.

The tame disposition of *P. (M.) natalensis* and its lack of aggression are probably the reason for its ready retreat from *Rattus rattus*; it may also be linked with the social life of several families living together in a burrow and the large litters. The usual number of young is between 10 and 12 but the total recorded range is 3—19 per litter. Since the female's gestation period is less than one month and she can become pregnant again immediately after giving birth, and the young are capable of breeding at the age of 3½ months, there is the potential of each rat multiplying itself by five each month. When this potential is realized it is hardly surprising that large hordes occur. However, vast increases in numbers are only sustained for a short while, because this species is a seasonal breeder and the majority of young are born within a short period—although some breeding is going on all the year.

In the southern latitudes there is a single breeding peak at the end of the rains, with the young most numerous in the early dry season (see Pirlot, 1953, 1954; Chapman *et al.*, 1959; Coetzee, 1965). This pattern differs from that of most other savanna rodents and it would be interesting to know where the advantage lies in having the young at a different time from other species, particularly when a heavy toll can be expected after the dry season fires.

Further north the pattern is less clear; Misonne (1963) found two quite different patterns of biannual breeding in two equatorial localities in eastern Zaire (Congo).

In the Queen Elizabeth Park, yet another pattern is apparent (Delany and Neal, 1969). Here, some 90% of the females are pregnant at the end of the rains in May and some in June, and there is another breeding peak in October and November.

The high productivity of this rat and its role as a disease host, have led to its increasing use as an experimental animal (see Davis, 1963). It has been used for routine tests in research on plague, bilharzia, relapsing fever and cancer. Laboratory colonies in South Africa have been found to suffer a high incidence of stomach cancer.

They breed rapidly in captivity. The young are born naked and blind, their coat develops during the second week, the eyes open at 15—16 days and they are independent of the mother at 3 weeks—often just before she has another litter.



Age class calendar for *Praomys (Mastomys) natalensis* in Queen Elizabeth (Ruwenzori) National Park. Data from Neal (1967/8). Catches nearest centre of circle are the youngest, periphery are the oldest.

Soft-furred Rats, *Praomys* Rats (*Praomys* (*Praomys*))

Local names

Kadinzi (Kuamba, Lubwizi),
Idiakuru (Lutoro), Imbewa
(Kinyakyusa), Imbingi (Kinyika),
Nandalanendu (Kikinga), Hunja
(Kisambaa)

Species

Praomys (*Praomys*) *jacksoni** Uganda, Kenya and western Tanzania
Praomys (*Praomys*) *delectorum* , Tanzania and southeastern Kenya

The *Praomys* (*Praomys*) group is represented by two very closely related species in East Africa: *P. (P.) jacksoni* is a highly successful forest species, ranging from Cameroon to Kenya and down to Zambia and Malawi; *P. (P.) delectorum* is a smaller species principally found in the "Southern Forests" of Tanzania. The two species may intermingle somewhat in the vicinity of Abercorn but the separation between them is otherwise quite sharp, with the dividing line running between the Ufipa Plateau and the Poroto Mountains. The situation of the two species of *Praomys* in this area has been explored by Vesey-FitzGerald (1962b). He concluded that

"these ecologically isolated populations of *Praomys* may be explained by referring to past climatic changes and coincident spread and recession of forest habitat. It might be that the small Poroto rats are survivors of a very ancient eastward movement of a western fauna which subsequently during an early pluvial period became isolated. And the larger Ufipa and Abercorn material are the survivors of a subsequent wave".

This interpretation accords with the broad pattern of forest fauna distribution which was outlined in Volume I, p. 69. However, *P. (P.) jacksoni* seems to have extended its range further south than many other "recent" forest forms, which seldom penetrate further than the Kungwe-Mahari area.

Praomys (*Praomys*) are animals of humid, well shaded vegetation and are common in forest and secondary scrub in areas of high rainfall. They are however commonest in true forest and Delany (1971) caught most of his specimens in the older parts of the Mayanja Forest. They make concealed runways, which often pass under vegetable debris and roots. Their nests are built underground in short burrows, which are very often placed at the base of trees. The nest is about 10—12 cm across and is lined with fine material inside and with progressively coarser material surrounding it on the outside. Rahm (1967) published a photograph of one of these nests.

These rats are omnivorous and the stomachs usually contain both vegetable matter and insects. Commonly recorded foods are fruits, seeds, nuts and green matter. Vesey-FitzGerald (1966) has described feeding and associated behaviour

"It is crepuscular and nocturnal and shelters among all kinds of debris on the forest floor, where it is not subject to marked seasonal extremes. The home range of a group may be restricted to the vicinity of a single forest tree such as *Parinari*, which sheds its fruit on the ground. It collects the fruit by making sorties from a convenient shelter. The fruit is then carried back to the shelter, where the hard shell is gnawed at leisure in order to get at the kernel; the debris of continual feeding indicate that such shelters are used during a prolonged period possibly amounting to the life span of several generations. Indeed this

* *P. (P.) jacksoni* has often been classified as *P. morio* (a West African species).

method of livelihood is practised by other ecologically similar species. Since *Praomys jacksoni* is also very easily caught in traps baited with rat-meat, it may also be omnivorous in its diet”.

Praomys jacksoni has been found to be partly arboreal; of 369 animals trapped by Delany (1971), 141 were caught off the ground. He reports the results of an intensive field and laboratory study of this species. Especially remarkable are the monthly changes recorded in age structure. The criterion used to classify age classes in the wild is the degree of tooth-wear, but an attempt to correlate this with the actual age of laboratory-bred animals has been of limited value, because the standardized and relatively soft diet of captivity is thought to slow down tooth-wear and their life expectancy can also be doubled. For example, of the three age-classes plotted in the margin calendar, the first represents up to 48—91 day-old captives and the second up to 200—300 days. In the wild, probable life spans do not exceed one year and Delany remarks

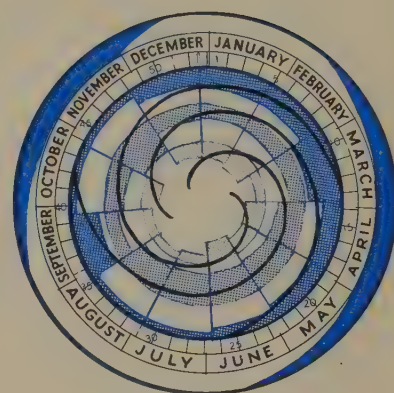
“the accumulated data on population structure and reproductive physiology of the small rodents in Mayanja Forest suggest a relatively rapid population turnover with little restriction on breeding”.

There are, however, reproductive peaks and the calendar summarizes the age class percentages published by Delany. The spiral lines trace some temporal age-progressions that can be extrapolated from the data, although it should be remembered that the numbers of animals caught in some months are statistically inadequate. The numbers of *P. jacksoni* caught in various forests relative to that of the other small forest rodents range between 25% at Lemera, Zaire (Congo) (Rahm, 1967) and 32% at Mayanja (Delany, 1971). In East Africa, *Praomys* is an exclusively forest and forest edge rat, but in West Africa related species are reported to have adapted to cultivation within the forest zone and even enter houses. However, this subgenus has not been implicated in plague transmission, unlike *Praomys (Mastomys)*. Ticks, *Ixodes* species, have been found on *P. (P.) jacksoni* (Elbl *et al.*, 1967).

P. (P.) jacksoni has been found to breed continuously, but a greater degree of periodicity appears in populations living in true forest. Rahm (1967) attributes this to dietary differences but it is also possible that social density-dependent factors may affect periodicity.

The age class calendar reveals some fluctuations in the relative numbers of juveniles from one month to another at Mayanja. Eisentraut records a gestation period of 26—27 days for *P. (P.) morio*. By contrast Delany gives 34—37 days for *P. (P.) jacksoni*, an unusually large discrepancy for closely related species. Captive females sometimes mate again immediately after giving birth. Two to six young are born at a time, naked, pink and blind. The eyes open between the 11th and 16th day and the coat develops during the second week. The juvenile is independent at the age of one month, at which time the testes in the male begin to develop. The moult into adult pelage takes place at the age of two months and the animal is sexually mature at 2½ months.

As young *Praomys* and *Hylomyscus* can be difficult to tell apart, the hind-foot measurements become an important distinguishing character. At the weight of about 15 g the hindfoot of *Praomys* measures 20—23 mm exceeding that of an adult (25 g) *Hylomyscus*, which averages only 18 mm.



Age class calendar for *P. (P.) jacksoni* in Mayanja forest (data from Delany, 1971). Spiral lines trace hypothetical life-spans of age classes. Heavy stipple: older animals with worn teeth. Medium stipple: animals with medium tooth wear. Light stipple: young animals with minimal tooth wear.



P. (H.) stella.

**African Wood
Mice
(*Praomys*
(Hylomyscus))**

Family
Order
Local names
Mbule (Lukonjo)

Muridae
Rodentia

African Wood Mice

(*Praomys* (*Hylomyscus*))

Species

Praomys (*Hylomyscus*) *denniae*

Praomys (*Hylomyscus*) *aeta*

Praomys (*Hylomyscus*) *stella*

The wood mice have the soft grey-based fur that is typical of all the *Praomys* group, but they are distinguished by smaller size, short hindfeet and long thin tails. The three species are difficult to tell apart without examining the skull.

The role of wood mice as the arboreal branch of *Praomys* and the intermediate position of *P. (H.) denniae* between *P. (Praomys)* and *P. (Hylomyscus)* was discussed in the profile of this genus.

P. (H.) denniae is the largest species and is primarily a high altitude form with a discontinuous distribution. On Ruwenzori it is a dominant species living as much on the ground as in the branches; when I was ground trapping in the Ruwenzori Mountains at 3,000 and 3,500 m this species made up nearly 50% of my catch, and the British Museum Ruwenzori expedition also noted that it was very numerous (Thomas and Wroughton, 1909—10). *P. (H.) stella* is instead a rain forest species restricted in East Africa to the lower altitude forests of Uganda and western Kenya. *P. (H.) aeta* is primarily a Congo basin form, known from western Uganda.

The heights to which *P. (Hylomyscus)* may climb are not known, but it has been collected up to 9 metres above the ground and Delany (1971) found no tailing off of catches at his 3 m ceiling. The nests of *P. (Hylomyscus)* are made of dry leaves, banana and other vegetable fibre in tree holes, crevices in branches and palm or banana leaf-axils.

They are omnivorous and opportunistic feeders and I have noted vegetable and fruit pulp (white, yellow, green and orange), sometimes with traces of insects, and I have one record of a stomach filled with insects.

All species of *P. (Hylomyscus)* are truly nocturnal and are never caught by day. Heim de Balsac and Lamotte (1958) found that this subgenus constituted 8.5% of the diet of the barn owl, *Tyto alba*, in West Africa. This proportion probably gives a reasonable index of their abundance in suitable forest. In an optimum habitat like that of the Mayanja Forest near Kampala, *P. (H.) stella* represented 13.6% of Delany's total catch (1971). I have already noted the situation of *P. (H.) denniae* in parts of Ruwenzori where this species appears to be less strictly arboreal and is very dominant. However, it is possible that this species, like other *Praomys*, might be subject to population fluctuations. The abundance on Ruwenzori recorded by Woosnam (in Thomas and Wroughton, 1909—10 and confirmed by my own observation during June and December and those of Misonne (1963) can be contrasted with the findings of Loveridge (1942), who in January 1939 was able to catch only one animal at the same spot where Woosnam had found it "extremely common" in 1906 and where I trapped some 30 animals in 1966—67.

P. (H.) stella has been bred in the laboratory and the gestation and de-

velopment of the young have been recorded (see Delany, 1971). The gestation is about one month, with a range of 25—33 days; one to five young are born. Transparently pink and blind and weighing one or two grammes, their development is rather slower than that of *P. (P.) jacksoni*. Hair growth begins late in the second week of life and the eyes open between the 15th and 21st day. At the time when they leave the mother, at about 30 days of age, they weigh about 9 g. This species has a conspicuous breeding peak in Uganda with 71% pregnancies in June. There is probably another peak at the end of the year.

In the very wet West Uganda mountains, *P. (H.) denniae* may have a breeding season in July and August—when it is relatively dry—as a majority of animals coming into breeding condition have been collected in June, and a large juvenile population has been noted in October. In December another breeding peak begins at the start of the second spell of drier weather.

Aethomys kaiseri.



**Bush Rats,
Aethomys Rats**
(*Aethomys* (*Aethomys*))

Family	Muridae
Order	Rodentia

KEY TO AETHOMYS SPECIES

Aethomys chrysophilus

Very long tail, scaly.
Back reddish brown, fur
particularly sleek.

H. & B. 145 (125—162) mm
T. 165 (138—202) mm
Wt. 85 (63—105) g



Narrow skull

Aethomys kaiseri

Short tail, haired.
Back reddish brown,
rough fur

H. & B. 160 (150—165) mm
T. 140 (122—150) mm
Wt. 90 g.



Medium skull



Aethomys hindei

Medium tail, sparsely haired.
Back yellowish brown,
rough fur

H. & B. 155 (135—184) mm
T. 150 (121—186) mm
Wt. 100 (58—150) g



Broad skull



Bush Rats, *Aethomys* Rats (*Aethomys* (*Aethomys*))

Species

Aethomys chrysophilus

Aethomys kaiseri

Aethomys hindei

Aethomys have no obvious characteristics by which they can be identified in the field. They are rather variable in colour but all forms have a grey base to the fur, which is soft and sleek. Longer guard hairs in the rump are perceptible in some species, e.g. *A. kaiseri*. The belly is paler than the back and the feet are generally white. The general impression is one of ordinary rats. They seem in fact to provide a link between the generalized rats and the radiation of herbivorous rats in Africa. *Aethomys* rats might well be described as unspecialized herbivores.



They live in savanna except for the subgenus *Stochomys*, which is treated separately, but not enough is known of the species of this genus to be able to define their respective ecological niches with any great accuracy.

Aethomys chrysophilus is a woodland species, living in small social groups in termitaries and rocky outcrops where there are bushy foci. Vesey-FitzGerald (1966) describes its true home as rocky sites on slopes, where it is usually associated with *Acomys*.

Aethomys kaiseri uses similar shelters but is also found in many other sites such as cracks and cavities in the ground, under timber, in buildings or among boulders. This species appears to be less social and may therefore achieve a wider and more scattered distribution than the former species, with which it is sympatric, although Vesey-FitzGerald reports that the two have not been taken together.

Aethomys hindei is more of a grassland species but it is also common in cultivation and fallow. Southern and Hook (1963a) have caught it on the edge of swamp and forest and also under the trees in the Zika Research Forest, but these animals may have wandered in from the surrounding grassland, probably to forage for fallen fruit, for the species is certainly not a forest animal.

Aethomys feed almost entirely on vegetable matter, fallen fruits, seeds, grass seeds, leaves, buds and roots. Delany and Kanseriimuhanga (1970) offered quantities of various foods to captive *A. hindei*. Bananas and insects were refused. Over 40% of their diet was made up of the roots of cassava, *Manihot*, and tannia yam, *Xanthosoma*, 30% of seeds and the remainder was grass and sweet potato leaves.

Vesey-FitzGerald reports *A. chrysophilus* feeding on the fallen fruits of *Combretum* and *Grewia*.

Aethomys are mainly nocturnal and are particularly active in the early part of the night, but I have seen *A. chrysophilus* about just outside their holes in termitaries during the late afternoon.

They are presumably killed by small carnivores, by owls, hawks and snakes.

The gestation is 21 to 23 days and new-born young tend to stay permanently attached to the mothers' nipples for some days like *Grammomys*.

A. chrysophilus probably breeds throughout the year.



Target Rat
(Aethomys (Stochomys)
longicaudatus)

Family Muridae
Order Rodentia

Measurements
head and body
150 (120—172) mm
tail
215 (185—250) mm
weight
90 (60—104) g

Target Rat (*Aethomys* (*Stochomys*) *longicaudatus*)

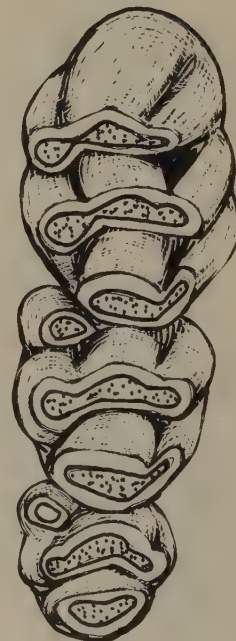
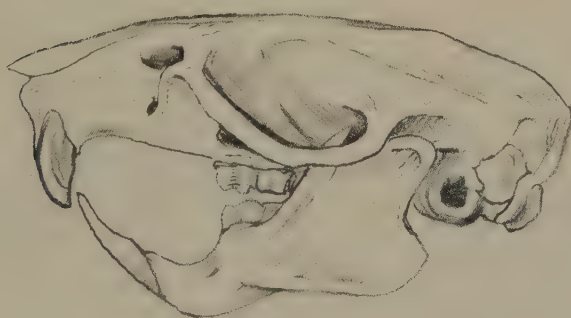
The target rat is a dark, reddish animal which gets its name from the long black bristles on the rump which have been likened to arrows in a target. One of the synonyms, *Mus sebastianus*, also refers to the martyr who was shot full of arrows. At any rate this is a very convenient field characteristic for the identification of the species.

A. longicaudatus is strictly a lowland forest species, only found from the Cross River in southeastern Nigeria to Bwamba in western Uganda. It is possible that this limited distribution reflects a recent adaptation to forest. Considering the southern African savanna-type distribution of other *Aethomys* species, it is not unlikely that this entry into true forest is a product of the climatic fluctuations that are known to have occurred in the southern areas of the Congo basin (see the discussion of *P. tetradactylus*, p. 66, Vol. I).

A. longicaudatus has been caught along the sides of streams and in swampy areas of the forest. It is also caught on occasions in banana plantations and in secondary growth around forest villages. Rosevear (1969) reports that 13 were caught in the Cameroons in "well-defined colonies in Oil Palm plantations". This is the only indication of their social organization. They are nocturnal and some have been noted as being caught in the earlier part of the night.

Its foods are mainly vegetarian; fallen fruit and green vegetable matter have been noted, and Hatt (1940) records three instances of insects being eaten.

Breeding appears to go on throughout the year.



KEY TO MUS

Skull and teeth	Colour	Well established species and measurements	Less well known forms or possible synonyms
-----------------	--------	---	--

Mus tenellus

**Long rostrum,
prominent
incisors**

brown back,
white belly,
short hairy tail
very pale form

H. & B. 64—68 mm
T. 34—40 mm

M. sorellus
M. wamae
M. gerbillus

Mus minutoides

**Short
rostrum,
very long
M1**

brown back,
white belly,
longer smooth tail

H. & B. 45—77 mm
T. 36—70 mm
Wt. 2.5—10.5 g

M. bellus
M. musculoides
M. gratus
M. birungensis

Mus triton

**Long
M1**

grey back,
white belly

H. & B. 57—93 mm
T. 42—55 mm
Wt. 7—16 g

M. emesi
M. imberbis
M. pasha
M. proconodon

Mus bufo

**M1 not
so long**

dark brown back,
buff belly

H. & B. 60—80 mm
T. 53—73 mm
Wt. 7—16 g

Mus minutoides.



**Mice
(Mus)**

**Family
Order**

Muridae
Rodentia

Mice (Mus)

The mice in Africa are a rather problematic group. They have no obvious relationship to any other African group but they are close to some Eurasian and particularly Indian species.

Misonne (1969) has suggested that *Mus* migrated from Eurasia independently of the original parent stock of the other African Muridae, probably at a later date. Misonne believes that there are 3 distinct groups within the genus and that representatives of each group are found in both Africa and Eurasia, which implies that three species of an isolated genus have managed to make their way into Africa independently. This is a controversial conclusion and the status of *Mus* in Africa is the subject of continuing investigation and debate.

Matthey (1966) in a study of their chromosomes has found great differences between species as well as polymorphism within *M. triton* and *M. minutoides* and he is of the opinion that these mice are actually in the course of speciation. His analysis of the chromosomes of over 200 specimens from various parts of Africa has revealed that some of the minor external differences that have been noted for very similar forms of mice are often reinforced by chromosomal differences that ensure reproductive isolation.

The key lists all forms of *Mus* described from East Africa. It is still too early to be certain of the status of many of these, but *Mus tenellus*, *Mus minutoides*, *Mus triton* and *Mus bufo* are well-established species and the latter three can frequently be caught together at high altitudes in western Uganda. *M. tenellus* is probably the most specialized species, while *M. bufo* is the most primitive and unspecialized. It is therefore interesting to find *M. bufo* restricted to the mountains of the Central Refuge (see footnote, overleaf). *M. minutoides* is the species with the widest distribution and has been caught in a range of habitats that include forest and semi-arid bush.

Mice are miniature rats, retaining the generalized body plan, locomotory versatility and omnivorous diet of their larger cousins. There is some evidence that the larger species may be more vegetarian than the smaller ones but all eat both animal and vegetable matter.

They tend to take shelter where they find it. For instance, it is not unusual to find safari baggage quickly tenanted by mice. All types of crevices and holes can provide a place for their cup-like nests. Watson (1950) describes the burrows of *M. minutoides* in Karamoja

"In soft, sandy soil the pigmy mouse will excavate short burrows, the mouth of which it fills, when in residence, with small stones, presumably to prevent the ingress of unwelcome visitors; the small stones must take time and much energy to gather. This peculiar habit is well known to the Karamojong and the name 'loyokomor', which is applied to the pigmy mouse, means 'pebble herdsman' from ekeyokon herdsman and imoru, small stone".

An identical habit has been recorded in the Australian *Leggadina*

"Some local mammalogists believe these are used as dew-traps. Since the air round the pebbles warms more rapidly as the sun rises than the pebbles themselves, dew forms on the pebbles by condensation. As the areas in which these mounds are found are quite dry except after heavy rains, these dew-traps solve the problem of water shortage".

Local names

Bunda (Kihehe), Sesi (Kinyika), Mbewa (Kinyakyusa), Ngorpo, Chanile (Kimakonde), Irutu (Kimwera), Kazura (Kirungu), Chivudu, Limwani, Sinamutali (Luhya), Chepchorn (Sebei), Mbuhu (Lugisu), Isimamori (Ateso), Loyokomoro (Karamojong)





* *Mus bufo* has recently been found on Mt Meru (Vesey-Fitzgerald, personal communication). It may therefore be expected in other montane localities.

They can often be trapped in the runways of larger dominant rodents or in close association with shrews. In any habitat they are seldom caught alone as the only species present. While *Mus* is unlikely to be directly dependent on any particular species or group of species, the investigation of their role within the rodent-insectivore community could be very interesting. It has been noticed, for instance, that in areas where there are population explosions of *Praomys natalensis*, the number of *M. minutoides* also rises and that it falls as the rats decline. Vesey-FitzGerald (1966) suggests that huge numbers of *Praomys* at such times provide a "predator shield" for *Mus* and other species that may also increase at this time, just when one might have thought that competition for resources was most keen. However, the quantity of food eaten by *M. minutoides* is a tiny fraction of that consumed by larger species and they might even benefit directly from the more wasteful feeders. Loveridge (1937) trapped an adult *M. minutoides* that was in good condition in spite of having been born with only 3 legs. Their enemies are numerous; snakes are possibly the most important, but they are frequently recorded from the crops of birds of prey. *M. minutoides* is almost exclusively nocturnal but both *M. triton* and *M. bufo* are about during the day as well and so fall prey to buzzards and other hawks.

All *Mus* species are easily kept and C. J. Jolly (personal communication) has had great success with *M. minutoides*, the animal breeding almost continually and producing litters of between 3 and 8 throughout the year. Vesey-FitzGerald describes a breeding peak during the dry season months in the Rukwa area, but Loveridge collected large numbers of pregnant females and nests containing litters during the wet season in southern Tanzania.



Total range *Mus minutoides*.



Mus minutoides.

House Mouse (*Mus musculus*)

The house mouse is an introduced species and its inclusion in the profiles of indigenous species might be thought to add still further to an already confusing situation. The house mouse is increasing rapidly in East African towns, although it is a relatively new arrival, being recorded for the first time in Kampala in the mid-sixties, where it has already become established in large numbers. This species has become a very serious pest in many countries and it is possible that it may become so in East Africa before long. The variety found in East Africa is a pale sandy coloured one with pale-grey belly.

Although it has a world-wide distribution today, living with man in all continents, under all climates, the wild house mouse stock probably originated in central Asia.

There is an extensive literature on this species. Useful information on its control is available in *Control of rats and mice* (1954, Clarendon Press, Oxford).

House Mouse (*Mus musculus*)

Family Muridae
Order Rodentia

Measurements head and body

72—92 mm

tail

70—86 mm

weight

13—30 g

KEY TO THE "HERBIVORES" OR ARVICANTHIS DIVISION

1. Upper incisors grooved			2
Upper incisors not grooved			3
2. Fur coarse, belly fur yellow-grey	<i>Pelomys</i>	(p. 623)	
Fur soft and lustrous, belly hairs with pure white tips	<i>Mylomys</i>	(p. 610)	
3. Lines or stripes on back			4
No lines or stripes			7
4. One dark line on back (sometimes faint)			5
More than one dark line on back			6
5. Dark brown forest mouse, shiny black soles to hindfeet	<i>Hybomys</i>	(p. 613)	
Paler grass and woodland species	<i>Lemniscomys</i> <i>griselda</i>	(p. 618)	
6. Four dark lines on back, highland species	<i>Rhabdomys</i>	(p. 615)	
Many stripes on back	Other <i>Lemniscomys</i> species	(p. 617)	
7. Fur coarse, strongly speckled	<i>Arvicanthis</i>	(p. 626)	
Fur long, silky iridescent, flat round face	<i>Dasymys</i>	(p. 607)	



**Shaggy Swamp-rat,
Dasymys Rat
(*Dasymys incomtus*)**

Family

Muridae

Order

Rodentia

Local names

Imbebwā (Kinyakyusa), Ikumba
(Kihehe), Ngerule (Kikinga),
Bunwe (Lugisu), Inya (Luhya)

**Measurements
head and body**

124—190 mm

tail

107—185 mm

hindfoot

27—33 mm

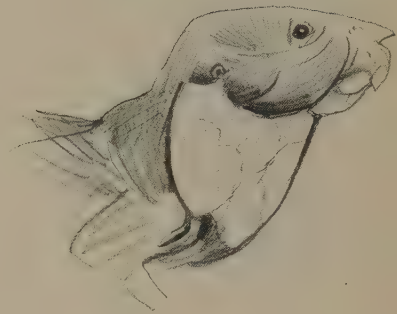
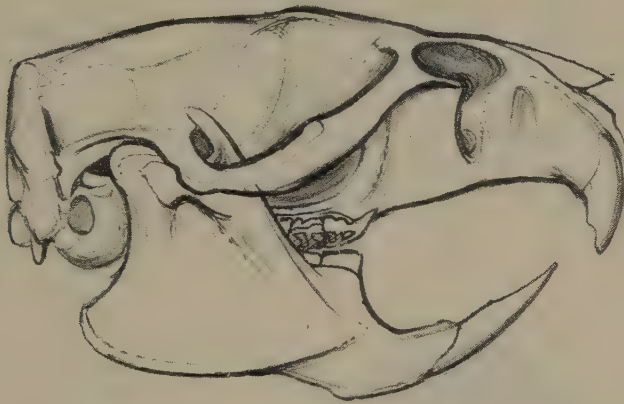
weight

82—125 g

Shaggy Swamp-rat, *Dasymys* Rat (*Dasymys incomtus*)

Although seventeen forms of *Dasymys* have been named, they probably represent colour phases or individual variations of a single species. In high altitudes long-furred, short-tailed forms occur, but Misonne has shown that even here there is a gradient in the body-tail ratio, which correlates with altitude. No races are recognized here.

Dasymys can be recognized by its rather limp, shaggy, fur and by its flat disc-like face with small eyes. The fur is dark brownish-grey and the plain orange incisors have a rounded cross-section. The skull is distinguished by the angled fore-edge of the zygomatic plate. The cones of the molars are in straight lines. This species has what appear to be immense salivary glands which form a collar round the throat.



Dasymys is known from the Pleistocene in the Transvaal, where a giant form was found. The genus probably represents a line of *Aethomys* stock that has adapted to marsh living.

The species ranges through most of the wetter grassy areas of Africa and is a very successful species in highland bogs and marshes, occurring up to over 4,000 m on Ruwenzori. Swamp rats are not found in really arid country and, although they are capable of living in relatively dry savanna, they are not numerous outside marshy areas.

Dasymys makes pathways through the grasses and mosses amongst which it lives and it probably shares runs with *Otomys*. Its nest is buried deep in a grass tussock and is made of fine grass. It has also been described as using holes in river banks in some areas but it usually lives among grasses growing in water-logged soil.

The food of these rats is probably entirely herbaceous and consists mostly of stems, roots, flowers and shoots of water-loving plants. Woosnam described *Dasymys* on Ruwenzori eating the flowers of *Helichrysum*, young rushes and apparently *Sphagnum* as well.

Dasymys do not come readily to baits, but they are often taken in traps laid in the runs that they share with *Otomys*. The feeding habits of these two



species are probably slightly different, *Dasymys* selecting softer, younger vegetation. Their activity patterns may also differ, for *Dasymys* is more diurnal. Owl pellets from Kigezi revealed seven *Otomys* skulls to two *Dasymys* and catches are often made during daylight hours.



The pre-eminence of *Dasymys* in marsh is very well documented by Misonne (1963). He found 34 animals per hectare in marshland and 2.6 in savanna. A comparison between the density and abundance of *Dasymys* and *Otomys* in three habitats is also interesting, suggesting that competition plays a role in keeping numbers of *Dasymys* down outside its optimum habitat.

The almost exact reversal of dominance between dry land and marsh is especially striking.

Dasymys is a very good swimmer, and Vesey-FitzGerald observed *Dasymys* living in the dense grass mat that floats over deep water in the seasonally flooded Rukwa Valley. All other rodents deserted the flood plains during the rains.

SPECIES	GRASS SAVANNA	HERBACEOUS GROWTH BORDERING MARSH	MARSH
<i>Dasymys incomtus</i>	2.6 p.h. (4.1%)	16 p.h. (12.6%)	33.9 p.h. (36.5%)
<i>Otomys irroratus</i>	23.3 p.h. (36%)	31.7 p.h. (24.4%)	16 p.h. (17%)

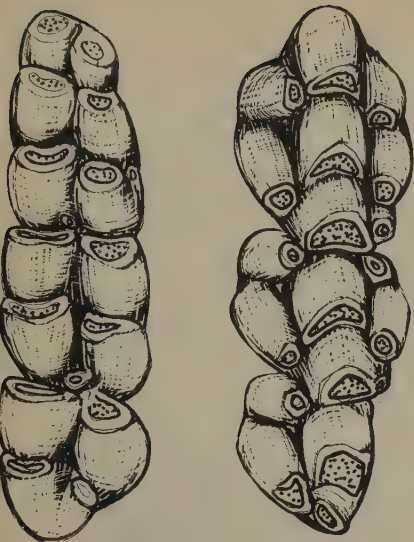
Density (numbers per hectare) and percentage abundance (of total small rodents and insectivores present) in Haut Ituri (from Misonne, 1963.)

At present *Dasymys*' feeding habits and habitat do not bring it into close contact with man, but as rice becomes more commonly grown in East Africa, it is possible that this species could become a nuisance.

Occasionally I have noticed egg-cases similar to those of lice clustered in great abundance on the hairs of this species' underfur.

The social and sexual behaviour of this species has not been studied and little is known of its breeding. The female has 6 mammae and is often rather greyer in colour than the male. Two to three young per litter are usual but four have been recorded.





Mill Rat, Mylomys Rat (*Mylomys dybowski*)

Mylomys, so called for its mill-like grinding teeth, is externally very similar to *Pelomys* and *Arvicanthis*. However, it has the distinguishing characteristics of having only three functional toes on the forefeet, grooved incisors and a shiny streaky back. The tail is peculiar in being well covered below with coarse white bristles but is shiny black and almost hairless above. There is a warm orange flush around the hindquarters. The powerful molar teeth are most unusual in having very prominent rounded cusps which face backwards in the upper jaw and forwards in the lower jaw.

Family
Order

Muridae
Rodentia

Measurements
head and body

154 (120—190) mm

tail

150 (104—180) mm

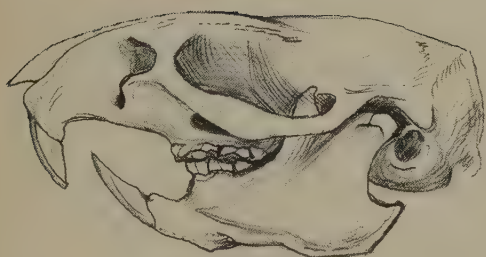
hindfoot

33 (29—36) mm

weight

100 (46—165) g

**Mill Rat,
Mylomys Rat
(*Mylomys dybowski*)**



Mylomys

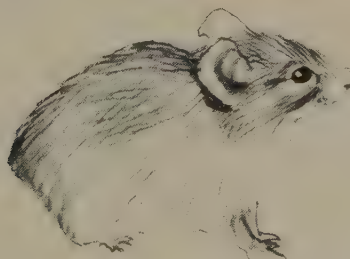
Miles
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Km

Mylomys dybowski is a tropical species, ranging from the Ivory Coast to Kenya and from the Lower Congo (Zaire) to Ruanda and western Tanzania. It has been found in a variety of moist grasslands often at quite high altitudes —2,400 m. These rats are very locally distributed and may be a dominant species in these little pockets. They have been noted especially in sword grass, *Imperata cylindrica* and in *Hyparrhenia* and also in upland grasses though not in marsh.

Their diet is apparently exclusively vegetarian and consists of green grass stems and leaves.

The most obvious competitors for the diurnal *Mylomys* are *Arvicanthis* and *Otomys*. Delany (1964b) has found this species dominant along the "Crater Track" in the Queen Elizabeth Park. Of some 150 rodents caught, 62 were *Mylomys*. This represents 75% of the herbivorous rodents, which included *Arvicanthis* (6) and *Otomys* (1), as well as *Lemniscomys* and *Tatera*. In this locality the *Imperata* grass is burnt in mid-August and the country is very sparsely bushed. It is very difficult to make out what factors could contribute to the local abundance of this species and its rarity elsewhere.

Breeding data from Delany and Neal (1969) suggest a biannual breeding season in western Uganda from March to June and from September to December.



Top right : base stems of *Imperata* grass after *Mylomys* have felled the stems to extract the pith in the basal 5 cm. Stems are nearly always eaten in a squirrel-like posture (C. Cheesman, personal communication.)



**One-striped
Forest Mouse**
(*Hybomys univittatus*)

Family
Order

Muridae
Rodentia

Measurements
head and body

130 (100—148) mm

tail

110 (85—120) mm

hindfoot

30 (24—31) mm

weight

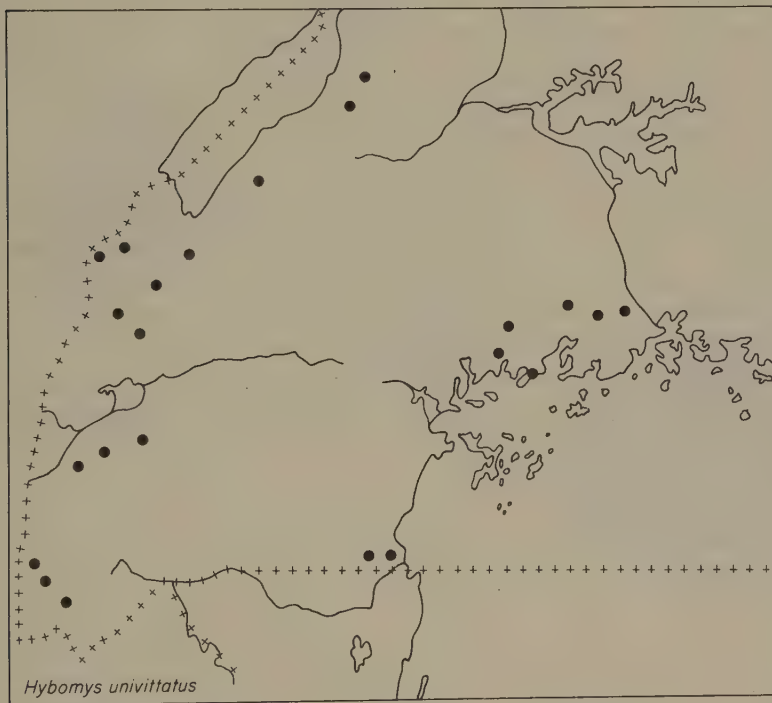
60 (30—64) g

One-striped Forest Mouse (*Hybomys univittatus*)

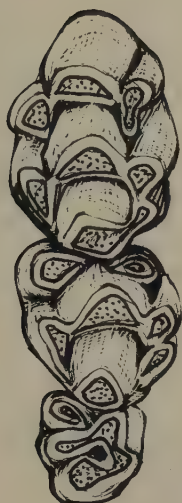
Hybomys is a mouse with a rich burnt sienna back, finely speckled with black and with an indistinct black line down the back. When ruffled the cream-coloured belly fur exposes a brown and grey base. The shiny black soles of the hindfeet look like polished patent leather and are highly distinctive.

Hybomys is a relatively unspecialized murid and, along with *Praomys* and *Hylomyscus*, is one of the commonest forest species. Structurally, *Hybomys* has affinities with *Rhabdomys* and other members of the "*Arvicanthis* division" in having broad inner cusps on the molars. It might almost be described as the forest equivalent of *Arvicanthis*, except that it is much less advanced. Nevertheless, its adaptation to the forest cannot be very ancient for the species has got no further east than the Victoria Nile and no further west than the Cross River in Nigeria, although a sibling species occurs in Ghana.

Within the main forest block *Hybomys* is very locally distributed. It is a strictly terrestrial species of the forest floor, preferring areas near rivers or swamps with abundant leaf litter and heavy shade. Apparently these mice do not make nests but shelter in rotting logs.



Food must determine the actual abundance of this species. It needs a mosaic of food-producing plants that can sustain it throughout the year, a requirement that is not as easily found in the forest as one might suppose. Of



some thirty stomachs of specimens from western Uganda, about a third had vegetable matter only (mostly fruit, or green and white pulps, which are presumably plant stems, shoots and leaves), about two thirds contained vegetable pulp with some insects, probably ants and termites, and one stomach contained insects only. They may also gnaw roots in the wild as they attack cassava plots along the forest edge.

Hybomys are noisy feeders, making loud clicks with their teeth as they eat; conceivably this could serve to advertise food in a habitat where it is likely to be locally concentrated but may only be available for a short while, after which other sources must be found.

I have trapped these rodents feeding on fallen fruit under a high canopy tree, *Antiaris*, which was being visited by many chimpanzees, monkeys and birds. At a later date, trapping in the same spot failed to catch any mice, presumably because no trees were fruiting there at the time. Likewise I have caught nine *Hybomys* in a single line of ten traps passing through a patch of fruiting *Aframomum*. The scatter of fruiting trees and shrubs on which *Hybomys* mainly depend might affect the animals' social behaviour, for they probably need a more extensive range than rodents living in closer touch with their food supply. Certainly they must be fairly mobile and the absence of nests might be due to the need to move about. They are captured in about equal numbers by day or night. Their escape behaviour in the forest is reminiscent of that of *Arvicanthis* or *Lemniscomys*; they are very difficult to see and they make very sudden leaps and a short rapid rush followed by complete immobility, after which they run away again.

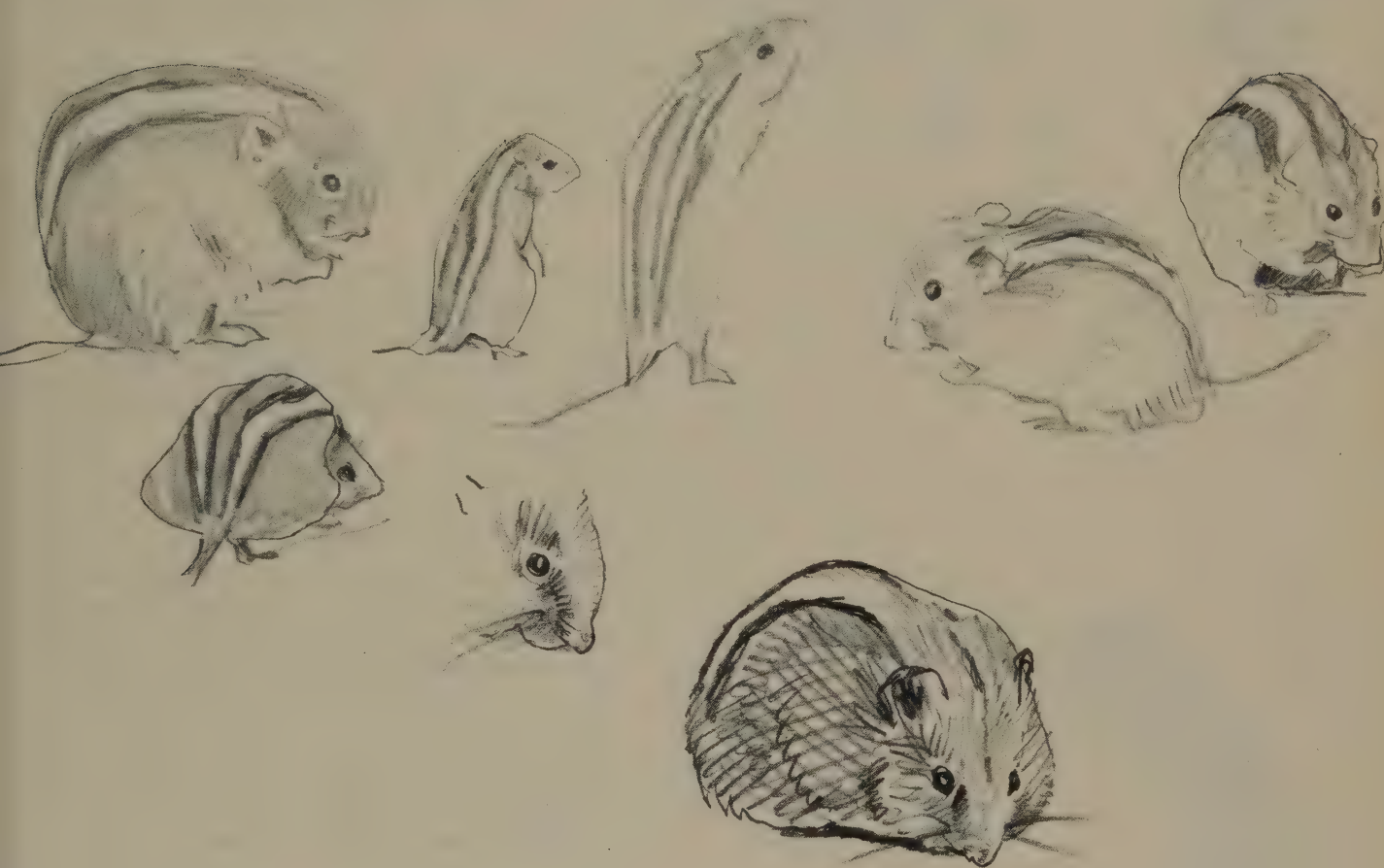
Hybomys are easy to keep in captivity and this together with their remarkably precocious and continuous breeding has led Petter and Genest (1967) to suggest that this mouse could be a useful laboratory animal. These authors have established that the gestation is exactly one month and they have described the development of the two to five young in detail. Females are capable of producing their first litter at the age of eleven weeks, although the average age is eighteen weeks. Continuous breeding in captivity is probably due to a high nutritional level. Rahm (1967) has found that wild populations of *Hybomys* in the eastern Congo (Zaire) breed continuously in cultivation where food is abundant throughout the year. In the forest, their seasonal breeding coincides with the main fruiting season, which is during the rains (February—May).

Four-striped Grass Mouse (*Rhabdomys pumilio*)

This grass mouse is immediately recognizable by the four black stripes along its back forming a pattern rather like that of the bush squirrel, *F. boehmi*. Animals from the Southern Highlands have particularly bright orange ears.

In East Africa this species is limited strictly to grassy uplands, moorland and the sub-alpine zone, from about 1,700 to 3,500 m; further south, however, *Rhabdomys* becomes more widely distributed and is found at lower altitudes.

Rhabdomys is known from the Pleistocene deposits at Olduvai and this



Four-striped Grass Mouse (*Rhabdomys pumilio*)

Family Muridae
Order Rodentia
Local names
Bunga (Kikinga), Malamala
(Kinyakyusa, Kinyika), Nyagalla
(Kihehe)

Measurements
head and body
90—135 mm
tail
80—135 mm
weight
30—40 g



could mean that the species was formerly more abundant than it is now or that the deposits were sampling the Ngorongoro uplands, an area where *Rhabdomys* is still a dominant species. However, the very patchy discontinuous distribution of *Rhabdomys* suggests either a specialized or a declining species; there is, however, no evidence of any particular specialization.

Rhabdomys is primarily a vegetarian mouse and, according to Misonne's study of murid dentition, it is most closely related to *Hybomys* and the *Lemniscomys*-*Pelomys*-*Arvicanthis* group. The teeth of these vegetarian rodents show a distinct trend towards more powerful cone-shaped cusps and broader molars. *Rhabdomys* is less advanced in this respect than *Lemniscomys* and *Arvicanthis* and it is apparent that these species tend to replace it in drier habitats. The increasing toughness of food in drier habitats may be one of the factors and the greater warmth of the lower altitudes may also favour the more recently evolved species away from the highlands. In this particular instance fire may also be a factor favouring the newer species (see the profiles of *Arvicanthis* and the Otomyinae).

There is also a broad pattern to which quite different mammals conform, namely that when formerly dominant types are replaced by more efficient species the latter tend at first to occupy only the most favourable areas, leaving the more remote or difficult habitats to the older species that often have a wider environmental range, having had more time to penetrate and adapt to peripheral habitats.

Rhabdomys has much the same habits as *Lemniscomys* and *Arvicanthis* and, in southern Africa, it shows some interesting regional differences in behaviour. Shortridge (1934) recorded them as climbing and occasionally sleeping in birds' nests in Namaqualand, a habit that is unknown elsewhere. He also noticed that the species was entirely replaced by *Lemniscomys* in the northeastern part of South-west Africa.

Foster (1966) trapped a small grassland area in Ngorongoro crater and found that *Rhabdomys* was the dominant species there. He caught 190 on 2.5 hectares in four days and nights. The associated vegetarians were 10 *Otomys*, 6 *Pelomys* and 4 *Steatomys*. This spectrum of species is similar to that found in high altitude grassland in southwestern Tanzania and contrasts strongly with the Uganda grasslands, where *Arvicanthis* and *Lemniscomys* are the dominant species. *Rhabdomys* damages growing tree plantations in South Africa and study of marked animals has revealed that an individual of this species can range over about 20 hectares.

In captivity *Rhabdomys* have produced 4 litters in a year; 4 to 12 young are born at a time and they are capable of breeding at the age of three months. Pregnant females have been recorded in Kenya during September.





**Striped Grass
Mice,
Zebra Mice
(Lemniscomys)**

Family Muridae
Order Rodentia
Local names
 Panya (Kiswahili), Mende
 (Luganda), Olurende (Lugisu),
 Livende (Luhya), Nyarubere
 (Lutoro, Lubwizi), Olutera
 (Lukonjo), Kadzora (Kipokomo),
 Kimuarees (Sebei), Eze (Kuamba)

Measurements
head and body

120 (98—140) mm
tail 120 (102—155) mm
hindfoot 23—32 mm
skull 27—32 mm
weight 50 (20—68) g

Lemniscomys griselda and
Lemniscomys striatus

head and body

100 (95—122) mm
tail 100 (94—124) mm
hindfoot 20—23 mm
skull 23—27 mm
weight 18—35 g

Lemniscomys macculus

head and body

105 (90—118) mm
tail 107 (95—133) mm
hindfoot 22—26 mm
skull 23—27 mm
weight 30 (23—41) g

Lemniscomys barbarus



Lemniscomys barbarus
(vertical)
Lemniscomys macculus
(horizontal)



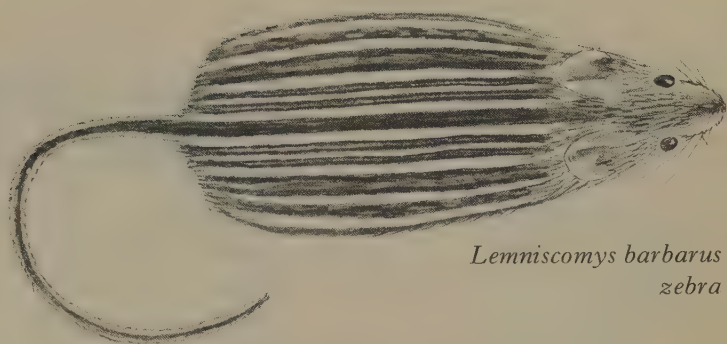
Lemniscomys griselda
(vertical)
Lemniscomys striatus
(horizontal)



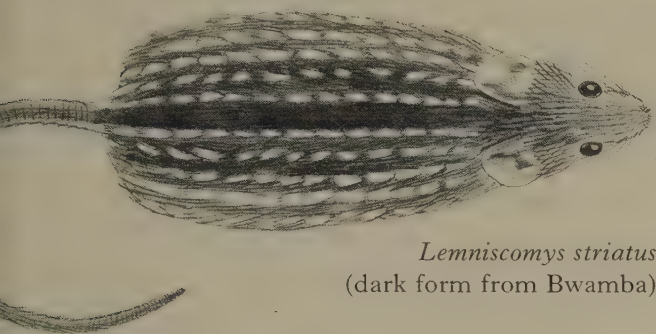
Rhabdomys (horizontal)
Isolated populations of
Rhabdomys (spots)
Pelomys minor
(vertical)



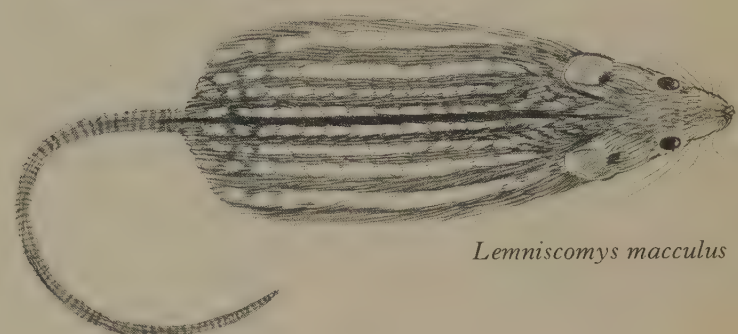
*Lemniscomys barbarus
fasciatus*



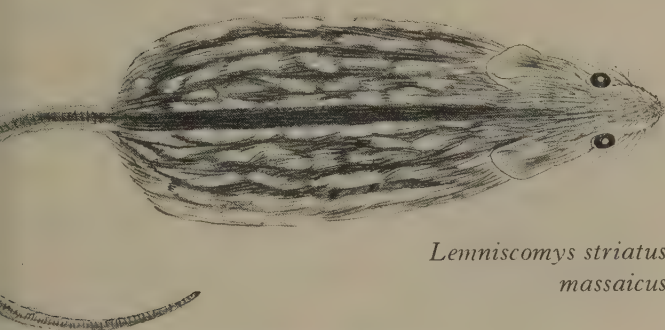
*Lemniscomys barbarus
zebra*



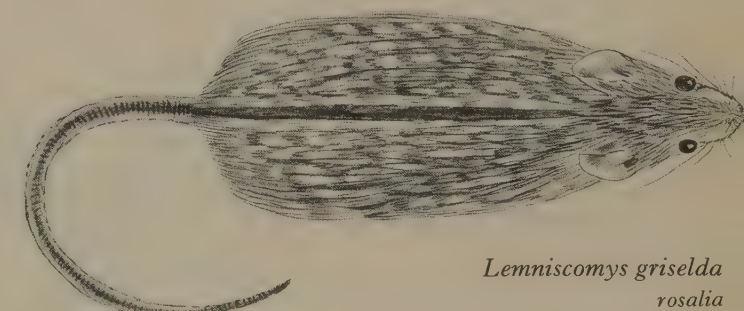
Lemniscomys striatus
(dark form from Bwamba)



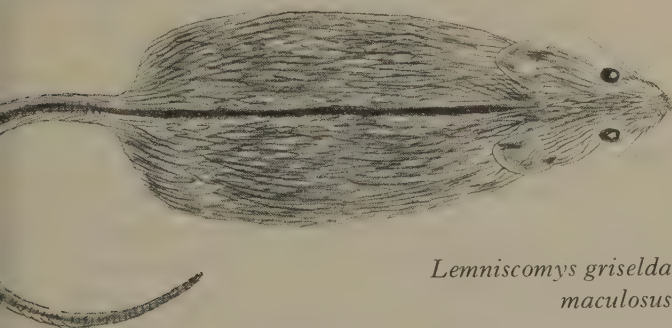
Lemniscomys macculus



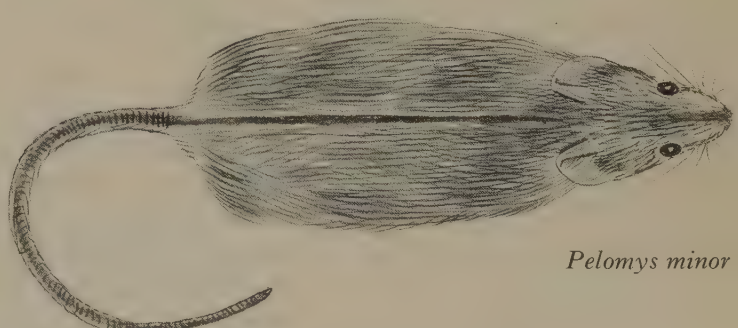
*Lemniscomys striatus
massaicus*



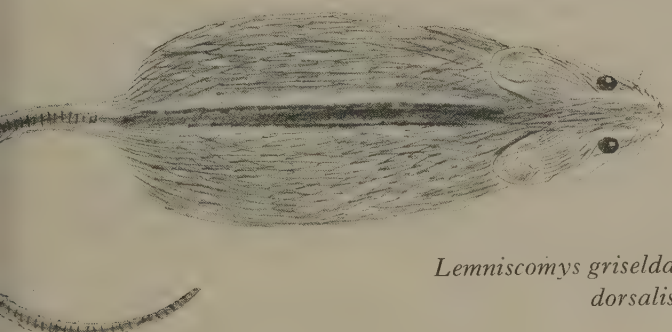
*Lemniscomys griselda
rosalia*



*Lemniscomys griselda
maculosus*



Pelomys minor



*Lemniscomys griselda
dorsalis*



*Rhabdomys pumilio
bechuanae*

Striped Mice, Zebra Mice (*Lemniscomys*)

Species

Lemniscomys griselda
Lemniscomys striatus
Lemniscomys macculus
Lemniscomys barbarus

Races

Plain-coloured species	<i>L. griselda</i>	
	<i>L. g. maculosus</i> (includes <i>mearnsi</i>)	South-east Kenya and northern Tanzania
	<i>L. g. rosalia</i>	Tanzania
Larger spotted species	<i>L. striatus</i>	
	<i>L. s. massaicus</i>	East Africa
	<i>L. s. ardens</i>	Highland form in central Kenya and northern Tanzania
Smaller spotted species	<i>L. macculus</i>	
	<i>L. m. macculus</i>	Ecological sibling species to <i>L. striatus</i> , Uganda, North-west Tanzania, western Kenya
Small striped species	<i>L. barbarus</i>	
	<i>L. b. zebra</i>	North Uganda
	<i>L. b. albolineatus</i>	Central Kenya
	<i>L. b. convictus</i>	South-east Kenya
	<i>L. b. manteufli</i>	Shores of Lake Victoria
	<i>L. b. spekei</i>	Tanzania

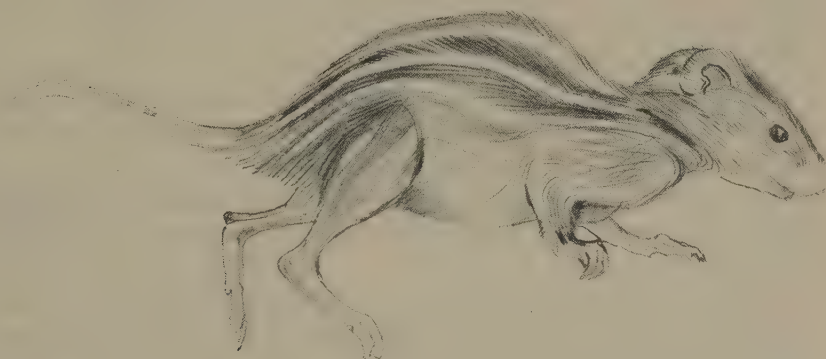
Lemniscomys is a complex genus containing species that are at different evolutionary levels. Furthermore the most primitive species; *L. griselda*, is a sibling species to *Pelomys minor* and is also closely related to *Rhabdomys* (see Misonne, 1969). *Lemniscomys griselda* is a species in retreat; it is rare through most of East Africa although it is sporadically common in *Brachystegia* woodland localities. It is abundant in southern Tanzania and throughout the rest of southern Africa, probably because it has no competition there from the more advanced *Lemniscomys* or *Arvicanthis* species:

L. griselda has a single dark stripe on the back on a speckled brown ground, a pattern that has been retained by the related *Pelomys* group and to a lesser extent by *Arvicanthis*. *L. g. rosalia* from Kiserawe, Tanzania, illustrated on p. 619, shows how a spotted coat can evolve from a grizzled one. A very similar pattern to this is found in a small population, *L. g. linulus*, from West Africa. This isolated relic group testifies to the declining status of this species. *L. striatus*, by contrast, is a dominant and successful species occupying a wide

variety of grassy habitats in tropical Africa, from sea level up to 3,500 m. The two *L. s. massaicus*, illustrated on p. 619, are extremes showing stronger and weaker pattern formation.

L. macculus has been regarded as a smaller, paler race of *L. striatus* adapted to semi-arid conditions, but it is widely sympatric with the latter without intermediates being known and Corbet (M/S) thinks that the recognition of two species is indisputable.

Considering the peculiar distribution of *macculus* it is difficult to see what physical barrier could lead to the isolation of the ancestral population. One must conclude that the division of their common ancestral stock was promoted by an ecological contrast that must have been more extreme than is apparent in the mosaic of vegetation and climate of present-day Uganda. Nonetheless, *macculus* generally occupies much drier habitats than *striatus* and it may have been very recent cultivation or pastoral practices that have led to the overlap of species. *L. macculus* is one of several animals typical of a drier Sudanic fauna which are found in a belt running south into Ankole and Karagwe. Like the hartebeeste, *Alcelaphus buselaphus jacksoni*, which was discussed in Vol. I (p. 79), this mouse may have been favoured by the 14th-century Hima migration. The pastoralists probably created a corridor of fire climax grasslands where none existed before, and it is in this corridor that *macculus* seems to be most distinctly recognizable.



Young *L. striatus*.

The separation of *macculus* and *striatus* into what should be ecologically distinct niches might be looked at as some sort of dress-rehearsal for the speciation of *Lemniscomys barbarus*. Furthermore, is it not possible that *L. macculus* had actually entered the *L. barbarus* niche in the eastern part of Africa, only to be later displaced by the more highly evolved *L. barbarus*, which had evolved elsewhere, presumably to the west? If this was the case, *L. macculus* might represent an incompletely evolved population that formerly ranged further north, but which has largely become replaced by *L. barbarus* and is now in the last stages of being "squeezed" between two dominant species. There is in *macculus* a tendency towards a narrowing of the mid-dorsal line and the amalgamation of spots into stripes, a process whereby the camouflage is rendered lighter and more appropriate to a more open, sun-bleached type of grassland. Like *L. barbarus*, *L. macculus* is of appreciably smaller size than *Lemniscomys striatus*.



L. barbarus is a species typical of the drier savannas and steppes that border the Sahara and extend through a large area of northeastern Africa. Its evolution from *L. striatus* is suggested by a Nigerian population, *L. b. fasciatus* (the pattern of which is shown in the key p. 619). Once again, ecological rather than physical barriers may have encouraged the separation of this boldly striped species. The savannas in which *Lemniscomys* live grow under such various climatic conditions and at such different altitudes and latitudes that the differentiation of the niches occupied by species can only be defined in the areas where there are more than one form. Thus in areas where *barbarus* and *striatus* co-exist the latter tends to live in the moister drainage lines, the former in scrubby areas where there is rapid run-off. *L. griselda* has adapted well to the *Brachystegia* woodland zone, with small groups centring on tertiary thickets. It is common along the edge of grassy pans or "Mbugas" within this zone. Here too, *L. striatus* tends to follow the more permanently moist drainage lines under shrubby herbs and other thick vegetation.

All the species make grass nests lined with a fine tow of shredded grass. Well-defined runs lead through the grass, where small piles of cut grass stems provide evidence of their feeding. In addition to grass stems and leaves, *Lemniscomys* eat seeds and most cultivated crops and at times they may eat insects.

Lemniscomys is partly diurnal and like *Arvicanthis* seems to have a short, intensive feeding period, but apparently at a different time, eating mostly in the evening and early morning. Lenkiewicz and St Giron (1964) found that captive *barbarus* and *striatus* in Paris were mainly crepuscular but exhibited spasmodic activity during the night as well.

Lemniscomys may live at relatively high densities. Misonne has found an average of 11.6 per hectare in the grass savanna of the Haut Ituri, where they constitute 18.4% of the small mammals present. *Otomys irroratus* is perhaps the main competitor in this area and habitat, representing 39.9%. In localities where neither *Otomys* nor *Arvicanthis* are dominant species, the density of *Lemniscomys* is much higher; for instance, Rahm (1967) caught up to 32.9% *L. striatus* in some Kivu localities.

They do not seem to be gregarious, although several can be seen close together while feeding. Recorded predators are mainly hawks, *Melierax*, *Buteo auguralis* and *Cerchneis*. Heim de Balsac and Lamotte found that *Lemniscomys* were seldom present in barn-owl pellets.

Lemniscomys have two distinct breeding seasons in the Queen Elizabeth Park, which coincide with the rainy seasons. Similar peaks have been recorded in western Africa by Petter, Chippaux and Monmignant (1964). These authors established that the female of *L. striatus* has an oestrus cycle of six days, a gestation of 28 days and that a single pair can produce 21 young with 4 litters in less than 4 months. The usual number of young born at a time is 4 or 5, but up to 12 have been recorded.

The new-born weigh 3 grammes and are covered in short hair; the pattern is well marked at birth. The eyes open at the age of one week. The adult weight of 50 g is achieved at the age of 5 months, but females are thought not to breed until they are a year old, in spite of displaying sexual activity from the age of 2 months.



Age class calendar for *Lemniscomys striatus* in Queen Elizabeth (Ruwenzori) National Park. Data from Neal (1967/8). Catches nearest centre of circle are the youngest, periphery are oldest.

Creek Rats (Pelomys)

Species and Races

Pelomys minor

Pelomys fallax

Pelomys isseli isseli

Pelomys isseli hopkinsi



Pelomys fallax.

Creek Rats (Pelomys)

Family Muridae

Order Rodentia

Local names

Mende (Kisambaa), Sinza (Kikami),

Siangi (Kinyakyusa)

Measurements

head and body

145 (133—165) mm *Pelomys fallax*

tail 150 (133—167) mm

hindfoot 32 (29—36) mm

weight 95 g

head and body

100—115 mm *Pelomys isseli*

tail 143—165 mm

hindfoot 29—32 mm

weight 60 g

head and body

100—125 mm *Pelomys minor*

tail 100—150 mm

hindfoot 22—30 mm

weight 50 g



P. fallax.



Pelomys resemble *Arvicanthis* but can be told apart by their grooved incisors. The genus is also closely related to *Lemniscomys*, *Rhabdomys* and *Hybomys*.

The isolated Kigezi population *Pelomys isseli hopkinsi* lives in high altitude grassy bogs and the Ssesse Islands *P. isseli isseli* along the edges of papyrus swamps. Where it occurs, *Pelomys isseli* can be quite common, but these races are probably relics of a non-competitive population that has now become limited to very marginal habitats in mountain and island refuges. Other closely related forms occur in the Ethiopian mountains.

It is very difficult to tell *Pelomys minor* from *Lemniscomys griselda*. Two groove-toothed animals from the Southern Highlands (Ruanda Valley, near the Zambian border) probably belong to this species but as one is very old and the other is subadult their exact status remains uncertain.

The principal species *P. fallax* is essentially limited to the southern savannas where it is generally associated with damp valley bottoms and marshes, but its habitat seems to vary somewhat with the locality. In many parts of eastern Africa *P. fallax* is only found at higher altitudes.

Vesey-FitzGerald (1966) describes the range of habitats occupied by this species in the Ufipa-Rukwa area:

"*P. fallax* usually occurs in rather damp environments where access to water is possible throughout the year, and where the overhead shelter is not normally destroyed by fire. Specimens have been collected in flood plain grasslands, mixed woodland, cultivation, edges of bogs, stream sides, the perimeter of forest, in termitaria thickets and rubbish heaps in gardens—habitats which it usually shares with other species".

In some places *P. fallax* become semi-aquatic and Shortridge (1934) describes them in the Okavango swamps: "*Pelomys* were often observed sunning themselves like water voles on the fringe of the reed-beds, now and again taking short plunges into the water from one patch of vegetation to another. They were rather wary and on alarm disappeared behind the reeds".

Notwithstanding its ability to be semi-aquatic, the animal is not much modified for swamp life anatomically, and it may well be that the adoption of this habit is partly the product of competition. Perhaps the *Pelomys* genus represents the surviving wing of a once more versatile and widespread group which has since been replaced by more advanced species in the better habitats. Its nesting habits prejudice its survival in grasslands that are regularly fired, for they are not built in burrows but hidden in the bases of tussocks at ground level. They are made of fine grass or the shredded leaves of coarser reeds. Rahm (1967) illustrates one.

Pelomys is diurnal and eats the leaves, shoots and stems of various grasses and swamp vegetation; it has been reported to damage sugar cane, elephant grass and even to fell maize stems.

As Vesey-FitzGerald remarks, *Pelomys* associates with a wide variety of other rodents. At the wettest end of the catena is *Dasymys* and at the drier end *Lemniscomys* and *Arvicanthis*. In between *Otomys* and *Mylomys* sometimes share the habitat. Although *Pelomys* and *Arvicanthis* are often found in the same area, little is known of their interaction nor of the degree of overlap. In parts of East Africa and particularly in eastern Zaire (Congo), *Arvicanthis*

appears to replace *Pelomys* in the rodent spectrum. However the complexity of the problem is best illustrated with figures assembled from the work of Rahm (1967) and Misonne (1963) in eastern Zaire (Congo). In a study of the rodents of the Kivu region, Rahm found *Pelomys* represented 2.53% of his entire rodent and soricid catch. But these were mostly caught in an area of secondary bush and cultivation by the shores of Lake Kivu at 1,600 m altitude. In this area there are no *Arvicanthis* and Rahm's figures make an interesting contrast with those of Misonne for roughly equivalent habitats in Haut Ituri, where *Pelomys* is absent, but where there is a very similar range of associated rodents.

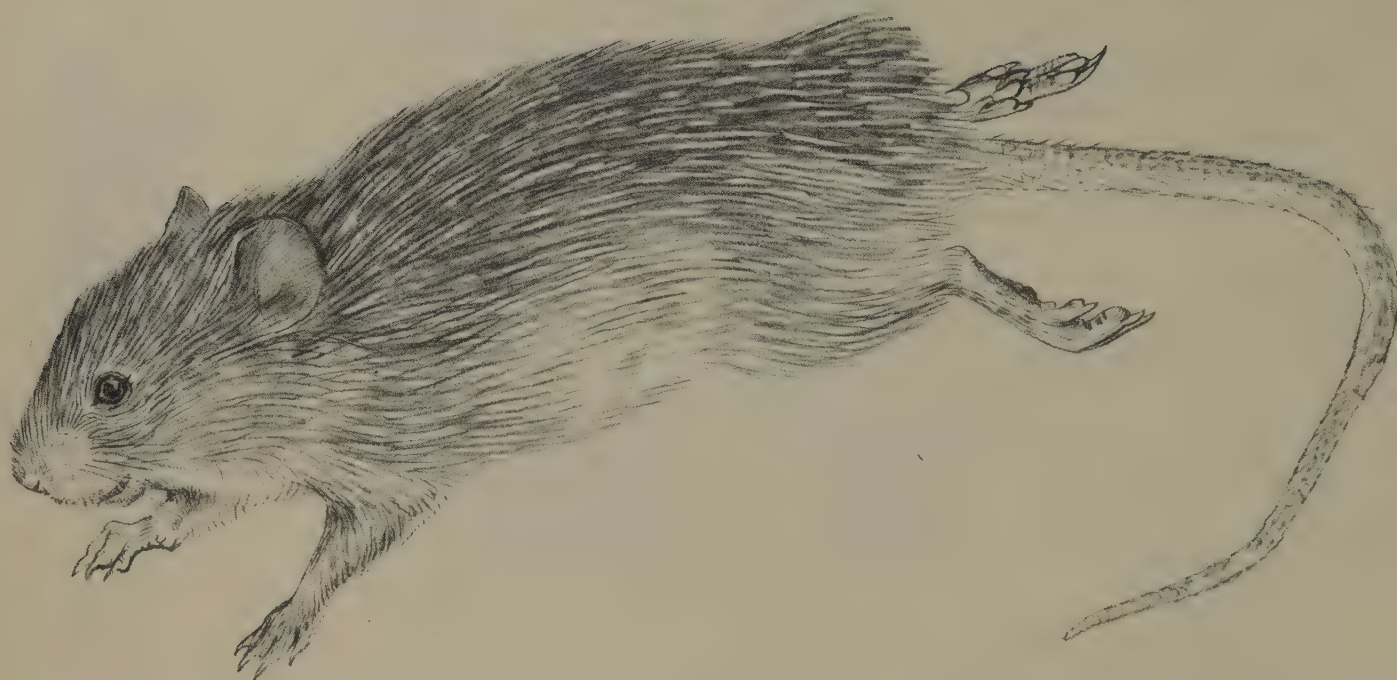
The table below lists the vegetarian rodent species in both areas and compares percentages.

SPECIES	HAUT ITURI, EDGES OF VILLAGE AND BORDER OF MARSH	BUHENGERE, SECONDARY BUSH AND CULTIVATION BY LAKE KIVU
<i>Pelomys fallax</i>	—	19
<i>Arvicanthis</i>	29	—
<i>Mylomys</i>	—	2
<i>Lemniscomys</i>	8	52
<i>Otomys (irroratus)</i>	40	3
<i>Oenomys</i>	12	13
<i>Dasymys</i>	11	11

Percentages of herbivorous rodents from two localities in eastern Zaire.
Data from Rahm (1967) and Misonne (1963).

The comparison begs a variety of questions that might be usefully pursued in those East African habitats where a melange of species occurs and where one might postulate a direct competition for resources and space by similar species.

Two to three young are born at a time. Ansell (1960a) records juvenile and subadult *P. fallax* throughout the year in Zambia and thinks there may be no fixed breeding season. Moults in *P. isseli hopkinsi* are very conspicuous, as irregular patterns are formed by new warm orange-tipped hairs appearing in patches next to worn pale tawny-tipped hairs.



**Unstriped Grass
Rats,
Arvicanthis Rats
(Arvicanthis)**

**Family
Order
Local names**

Mese (Luganda), Mbeba (Lutoro),
Mbabu (Kuamba), Myera (Kisebei,
Lugisu), Injhi (Tereki), Engeki
(Luhya), Manyaret (Kimasai),
Egurumu (Mteso), Emir
(Karamojong)

Muridae
Rodentia

**Measurements
head and body**

145 (106—204) mm

hindfoot

28 (23—32) mm

weight

78 (50—120) g

tail

100—152 mm (The tail tends to
be longer proportionately in
Arvicanthis lacernatus which is on
average a smaller species)

Species

Arvicanthis niloticus :

dark heavily speckled back, grey belly and proportionately shorter tail.
(May include *abyssinicus*, *nubilans*, *nairobae*, *rubescens*, *centrosus*, *tene-*
brosus, *reichardi*, *chanleri*.)

Arvicanthis lacernatus :

yellowish, less speckled back, white belly and proportionately longer
tail. Generally a smaller and more lightly built animal. (May include
muansae, *neumanni*, *pallescens*, *virescens*, *reptans*.)

Unstriped Grass Rats, *Arvicanthis* Rats (*Aryicanthis*)

Arvicanthis rats are distinguished by their rather harsh grizzled coat and smooth incisors. The existence of two distinct but sympatric forms has been recognized for many years, but it is still difficult to understand the nature of their relationship. The only structural differences are a tendency towards longer tails and a shorter tooththrow in the white-bellied form. This rules out the possibility of the differences being due to polymorphism within the species. In Uganda the white-bellied forms are rather rare and tend to be found in drier areas than the very numerous and widespread dark ones. This could suggest that the white-bellied form is being supplanted. An ecological difference between populations has been observed by Watson (1950) in Karamoja, where he found dark *Arvicanthis* on the plains and the white-bellied form extremely numerous on the grassy spurs of Mt Kadam. In the drier and more easterly areas of Kenya and Tanzania, Vesey-FitzGerald (personal





Arvicanthis

Common and dominant
Present but not dominant
Sub-fossil recorded



Arvicanthis lacernatus



Arvicanthis niloticus

communication) has found the yellow-backed light-bellied populations dominant and the dark *niloticus* forms restricted to moister habitats in Kenya and to the wetter western half of Tanzania. The mapping of records has followed the synonymy suggested above but very many races of *Arvicanthis* have been described and the genus is in need of revision.

Arvicanthis is essentially a grass-loving species and its main home seems to be the northern savannas. It has a scattered distribution through parts of Tanzania and Zambia and is unknown from southern Tanzania and all of southern Africa.

Arvicanthis is certainly one of the most highly evolved of herbivorous murids and it is probably in the process of expanding its range. *Pelomys fallax* and *Lemniscomys griselda* between them probably occupy the *Arvicanthis* niche in southern Africa (although the former species is more dependent on water). Where these species are present in the same habitat as *Arvicanthis* the latter is more numerous, but in many parts of eastern Africa altitude tends to separate *Arvicanthis* from *Pelomys* for the former has apparently not adapted to living in the highlands.

Arvicanthis are commonest in the grasslands of Uganda where they are a dominant species. They tend to live under a dense herb mat, where they construct long tunnels at ground level radiating out from their holes. These they may dig in soft earth, but more often they rely upon the minor modifications of natural crevices in cracked soil, under fallen trees or rocks, in termitaries or among roots or, occasionally, in local huts. They make nests of fine grass in these holes and also may make nests in the base of grass tussocks.

Arvicanthis are primarily diurnal. They feed mainly on the seeds, leaves and shoots of grasses. Where they live in stands of *Digitaria abyssinica*, they reach high densities because the shoots and leaves of this grass are a favourite food. They also live in and eat *Imperata* grass, and Hopkins reports that the shoots and leaves of *Amaranthus polygamus* and *Bidens pilosa* are favoured. They also attack some crops, mainly stored grain, cassava and sweet potatoes. The presence of piles of cut grass indicates their feeding areas. They do not normally venture into modern concrete or brick buildings but do enter grass huts and grain stores.

These rodents are gregarious but the number of rats within their holes tends to be regulated. Vesey-FitzGerald (1966) found the same number of animals in small groups of holes as he did in the extensive "warrens" that form where large groups of well-established holes have joined up over years of occupation. Misonne (1963) found 20 *Arvicanthis* per hectare in Haut Ituri, but this moist habitat was shared with large numbers of *Otomys*. It is likely that densities can be much higher in areas where *Otomys* is absent or rare and during wet seasons densities must certainly be much higher. Watson reports a large regular annual increase of *Arvicanthis* in Karamoja with the rains, followed by a sharp decline during the dry season. It was thought that the abnormal rains in Karamoja during 1955, stimulating a particularly rich growth of grass, were responsible for an enormous increase in the numbers of *Arvicanthis*.

One facet of *Arvicanthis*'s success seems to lie in its ability to recoup its numbers after the annual dry season depletion. Its faster movements and its larger number of young must make it decisively superior to *Otomys* wherever

both species are badly hit by seasonal fires and exposure to predators. *Arvicanthis* may therefore be a dominant or expanding species because of increased use of fire in contrast to *Otomys* which appears instead to be a declining genus. In this connection it should be mentioned that sword grass, *Imperata*, which is a favourite source of food and shelter for *Arvicanthis*, is a fire climax species.

They evidently rely on their very good camouflage for safety; typically one only sees the animal just before treading on it, as it breaks away at the last moment to bolt along its run.

Arvicanthis feed mainly in the afternoon which happens to be a siesta period for numerous birds of prey and small carnivores. It is interesting that the recorded predators of this rat are all species that are commonly active during the heat of the day; i.e. the mongoose, *Herpestes ichneumon*, the black-shouldered kite, *Elanus caeruleus*, the crested hawk eagle, *Lophaetus* and the lizard buzzard, *Kaupifalco*, and snakes including *Naja* and *Psammophis*. In spite of this evidence of heavy predation it is possible that losses are less heavy in the afternoon than during the early morning or evening, when the greatest number of predators are about.

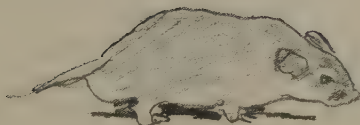
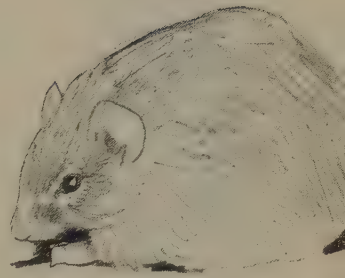
Arvicanthis have been reported to be carriers of the plague bacillus in the Congo, but Hopkins doubted the accuracy of these reports for this species. In a series of experiments Weinbren and Mason (1957) showed that *Arvicanthis* is able to circulate Rift Valley Fever virus without succumbing to the infection. They suggest that the species may be a natural host for this disease.

Some idea of the numbers of *Arvicanthis* in Buganda is shown by the figure of 20,000 rats reported killed in 1920 in and outside Kampala. (Baker in Hopkins M/S.) There are no longer the huge numbers of *Arvicanthis* round Kampala that there were in 1920. This is probably due mainly to the regular cutting of grass by the municipal authorities.

Arvicanthis have proved easy to keep in captivity and have been used as laboratory rats. Individuals have lived up to nearly seven years.

It is thought that several litters might be born during the wet season and as the numbers of young range from 4 to 6 the species' fecundity may be an important factor in its success. Weinbren and Mason (1957) experienced difficulty in getting *Arvicanthis* to breed in the laboratory, until they supplied nesting boxes and a rich diet of greenstuffs. Green food might therefore provide a biochemical trigger to seasonal breeding in the wild.

The young are born in the nest at about the same stage of development as the common rat and growth is rapid.



GENERIC KEY TO THE "CLIMBERS" OR *THALLOMYS* DIVISIONS

Wetter

Drier



- | | | |
|---|------------------|----------|
| 1. Mouth and nose bright red | <i>Oenomys</i> | (p. 643) |
| 2. Acacia-adapted species with
conspicuous dark mask around eyes | <i>Thallomys</i> | (p. 631) |
| 3. Tail tipped with hairs | | 4 |
| Tail not tipped with hair | | 5 |
| 4. Forest-adapted species.
Hindfoot relatively broad.
Larger (H & B 120—160) | <i>Thamnomys</i> | (p. 635) |
| Hindfoot relatively narrow.
Smaller (H & B 85—130) | <i>Grammomys</i> | (p. 637) |
| 5. Soft short fur, hair of belly
white with grey bases, pointed face
(arboreal forms of <i>Rattus</i> division) | <i>Praomys</i> | (p. 583) |

Acacia Rat (*Thallomys paedulcus*)

The arboreal Acacia rats are recognized by their long slightly hairy tail, sharp, curved claws on short feet and by their white belly and black eye mask; their ears protrude somewhat in the manner of the dormouse, *Graphiurus*.



Misonne (1969) considers this species the closest living relative of the extinct Miocene *Parapodemus* and that its teeth would place it in that genus if it were found as a fossil in Europe. It is certainly very close to the root stock of all African murids and the teeth also resemble those of *Aethomys*, *Thamnomys* and *Praomys*.

As an ancient form, *Thallomys* has escaped competition by adapting to a highly specialized way of life, and it has also retreated into a peculiar habitat that is not used by many rodents. It is interesting that it has been able to do this without any very great modification of form, remaining in many respects a typical rat.

Thallomys is principally a southern African form but with small popula-





Acacia Rat
(*Thallomys paedulcus*)

Family Muridae
Order Rodentia

Measurements
head and body

155 (120—162) mm

tail

130—210 mm

hindfoot

25—30 mm

skull

33—35 mm

weight

68 g

tions strung out through the Acacia bush and woodland country of East Africa (and recently recorded in Ethiopia). *Thallomys* lives almost exclusively in Acacia trees, especially *A. xanthophloa* and *A. tortilis*. It is very adept at running about among the thickest parts of the thorny canopy.

It nests in hollows but also constructs twig and stem nests that are placed in forks or on branches and which are lined with fine grass or shredded bark. Burrows among the tree roots are also used as shelters and pathways radiating from the trunk can often be discerned. The use of both arboreal nests and root burrows is curious and the animals seem to be highly responsive to local conditions. Some nests are used to sleep in by day and also to rear the young

but Roberts (1951) records that the earth burrows become a refuge from the South African winter cold.

Shortridge (1934) described peculiar structures built by this species in parts of southwestern Africa

“conspicuous masses of interlaced sticks are frequently built among the outer branches of trees (mostly acacias); these vary much in size and shape. The amount of material brought together to form a large nest would fill a wheelbarrow. These structures are not nests in a strict sense and do not seem to be occupied by day. Their significance is not clear, runways tunnel through them, and they may either be playing grounds or shelters into which to retreat when hunted by owls or other enemies. It was noted that considerable numbers of owls roost by day in the acacia belts fringing watercourses . . . The large outside shelters were observed mostly in small-leaved trees which did not afford much shade”.

Shortridge also observed what were apparently covered-in runways extending from nests. One of these structures was woven out of sticks and grass and

“extended like a parasitic vine up the trunk of a tree, measuring over six feet in height, another was built under the roof of an old native hut”.

Roberts noticed that *Thallomys* climbed into the thorny tangles after being disturbed out of their nests but that they dropped to the ground if harried any further. As, in some areas, annual bush fires must present a major hazard to this species, it is possible that terrestrial burrows allow them to escape being scorched in the branches. Where feeding is conducted in two different milieux perhaps it is also necessary to have two different bolt holes.

Activity generally starts in the evening shortly before dusk. The thorny canopy must help to shield these animals from owls and arboreal carnivores. Arboreal snakes such as *Dendroaspis* are probably important predators.

Their foods derive principally from the Acacia trees; buds, leaves, seeds and gum are supplemented by grass, seeds, berries, roots and the occasional insect, all of which are foraged very close to the parent tree or trees. Buds and leaves are the staple which is eaten in the canopy. Gum is gnawed directly off the bark. Acacia and grass seeds are mostly foraged for on the ground beneath the trees.

Acacia trees do not seem to be a chosen habitat for squirrels, and *Thallomys* seem to have filled a relatively empty niche. I once mistook a dormouse, *Graphiurus*, for *Thallomys* when I saw the animal climbing about in an Acacia in the evening. Apart from the tail there is some superficial resemblance in the colouring and facial pattern of the two species. *Galago senegalensis* is probably a competitor for suitable large hollows and also for acacia gum, but this is usually an abundant resource. *Thallomys* seems to have taken the *Thamnomys*-*Grammomys* adaptation a step higher into the trees and also a step further into the dry savanna.

Thallomys live in family groups or singly and not more than two pairs and their young have been found together in a single tree. The young stay with the parents in the nest until they are nearly fully adult in size. Up to four young are reared at a time and there is probably a breeding season centring on the rains. Pregnant females have been recorded in April and young animals have been caught in July and August.





**Broad-footed
Thicket Rats
(Thamnomys
Thamnomys))**

Family Muridae
Order Rodentia

**Measurements
head and body**

140 (123—160) mm

tail 175 (160—200) mm

hindfoot 24 (21—26) mm

skull 32—36 mm

weight 54—80 g

Thamnomys rutilans

head and body

145 (121—161) mm

tail 215 (180—222) mm

hindfoot 20—28 mm

skull 34 mm

weight 50—100 g

Thamnomys venustus

Broad-footed Thicket Rats (*Thamnomys* (*Thamnomys*))

Species

Thamnomys rutilans

Thamnomys venustus

The two species are most easily told apart by ruffling the fur of the belly. *T. rutilans* has hairs that are white to the skin with a buff wash to the tips. *T. venustus* has grey bases to the white hairs.

T. venustus appears to be restricted to the mountainous areas of the Central Refuge. It favours montane forest in the vicinity of rivers. *T. rutilans* is a forest species known from Guinea (Mt Nimba) to the Victoria Nile. It is



relatively common in areas of rank secondary growth and favours farms and other disturbed areas rather than the established forest. Both species are very arboreal and climb about, up to heights of several metres. Their nests have been found in various situations, in hollow trees, in forks or in the midst of

tangles. Rosevear (1969) describes the nests as

“constructed of very fine thread-like strips of grass aggregated into a sort of bag or purse some 6 inches by about 4 inches (150 × 100 mm) wide, very like some grass-weaver birds’ nests only not so skilfully woven”.

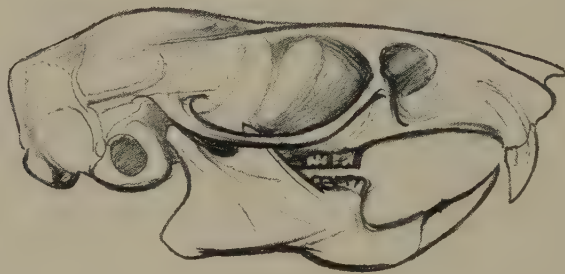
Their choice of foods probably resembles that of *Grammomys*; leaves and seeds have been recorded and cassava is eaten in captivity.

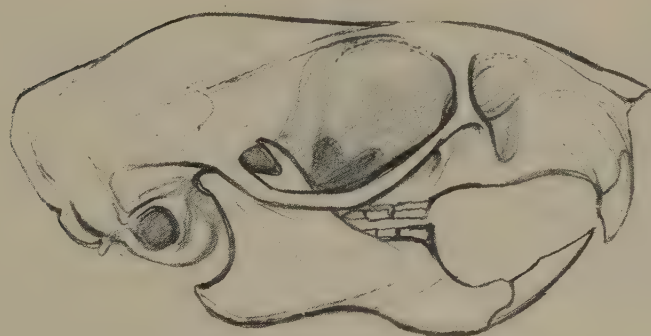
According to Misonne, the teeth of *T. rutilans* are extremely primitive, while those of *T. venustus* suggest that it is an offshoot from a *rutilans* stock. Both forms are probably in some sense relic species but, on the basis of distribution and relative abundance, *venustus* gives more the impression of a declining species than *rutilans*. After years of routine trapping in all habitats in the vicinity of Lake Kivu, Rahm caught a total of fifteen *T. venustus*, representing 0.64% of all murids and insectivores caught. *T. rutilans* represented 1.5% of Delany’s catch at Mayanja near Kampala (1971).

T. rutilans has recently been discovered to be the host to a *Plasmodium* resembling that living in *Grammomys dolichurus* (see Killick-Kendrick *et al.*, 1968). They have been implicated in plague transmission.

The gestation period of *Thamnomys* is thought to be about 25 days. The young are born with hair and with a peculiar condition of the incisors, having forked tips which are worn away by the time the animal is a fortnight old. This structure must assist the young to remain permanently attached to the nipple for the first two weeks of their life.

Delany (1971) found pregnant *T. rutilans* in Uganda during March. Female *Thamnomys* kept in laboratories in Europe bred continuously, producing 2–4 young every 5 or 6 weeks but females that were born in captivity could not be induced to breed.





**Narrow-footed
Thicket Rats
(*Grammomys
dolichurus*)**

Family

Muridae

Order

Rodentia

Local names

Kozo (Kisambaa), Nyalutanda
(Kihehe), Tangela (Kikinga),
Araraget (Kisebei), Sungama
(Lugisu), Esuba (Kuamba),
Kakumu (Lubwizi)

**Measurements
head and body**

85—130 mm

tail

130—205 mm

hindfoot

20—27 mm

weight

30—60 g



Narrow-footed Thicket Rats (*Grammomys dolichurus*)

- | | |
|-----------------------------|--|
| <i>Grammomys dolichurus</i> | (typical form) |
| <i>Grammomys cometes</i> | (localized; incipient species?) |
| <i>Grammomys macmillani</i> | (dry country form, possibly distinct species?) |

These thicket rats are slenderly built arboreal rodents with very long tails which are quite well haired at the tip. The belly fur is white. There is usually a buffy margin between the darker dorsal and belly fur. The rump is warmer in colour than the rest of the body but there is a very wide range of colours and numerous races have been described. Most of these varieties show a correlation between relative aridity or humidity and the tone and intensity of colour. The existence of intermediate forms makes definition of these populations very difficult and this has not been attempted here. However, one distinct population has received the attention of ecologists and taxonomists. This form was described as *Grammomys cometes* by Thomas and Wroughton

in 1908, a specific status that has been tentatively retained by Misonne (1968). Vesey-FitzGerald (1962) discusses this population which lives in the very wet montane forest area at the north of Lake Malawi. *G. cometes* may also occur in some less well-known localities further south, but all are high rainfall zones within a limited and well-defined area south of Lake Malawi. The Rungwe-Nyika area is of special interest to students of evolution in Africa for it shelters several distinct mammal and bird forms. All these forms are distinguished by dark colouring. Because there are no physical barriers between the Rungwe-Nyika populations and those living around them, one might expect a zone in which intermediate forms were found. This, however, is not the case for the elephant shrew, *Rhynchocyon cirnei hendersoni* (see p. 48), nor for the lark, *Mirafra africana nigrescens*, nor for *Grammomys cometes*. This population is generally very dark brown from head to tail with paler flanks and with white tufts behind the ear, but some are bright cinnamon like some West Uganda *dolichurus*. The measurements of these populations overlap but *cometes* is, on average, larger.

SPECIES	HEAD AND BODY	TAIL	HINDFOOT	SKULL
<i>cometes</i> (Rungwe- Nyika area)	112—129 mm ave. 123·3	142—195 mm ave. 173·3	20—25 mm	31—33·2 mm
<i>dolichurus</i> (surrounding areas)	95—129 mm 103·2—111·1	146—193 mm 162·3—166·3	20·5—26 mm	26·6—32·5 mm

That *Grammomys*, *Rhynchocyon* and *Mirafra* in this region all display incipient speciation without physical barriers to isolate populations distinguishes them from three other incipient species that are also endemic to the area but, which are, instead, relatively isolated from their nearest relations. These are the squirrel, *Funisciurus (Paraxerus) lucifer lucifer* (see p. 393), the longbilled greenbul, *Phyllastrephus flavostriatus alfredi*, and the canary, *Serinus burtoni melanochrous*. Most of the remaining forests are now being felled in this area and the water table appears to be falling in some areas too. Radical changes in the entire vegetation pattern have taken place in a few years. Vesey-FitzGerald (1962) thinks that:

“it is likely that in time these ecological races will intermingle and form a mixed population in which distinguishing characteristics . . . will be no longer recognizable”.



An intensive local study of these forms, whilst their habitat undergoes unprecedented change, would be of very general interest to biology.

Forms identified as *G. macmillani* are relatively small, the dorsal colouring is generally rather pale with grey or yellowish tints. These animals are sometimes caught very close to larger, brighter types but it is still uncertain whether they represent two distinct species or not.

G. dolichurus ranges from Guinea to the central Sudan, and from Kenya



Thamnomys (grammomys)

 *dolichurus*
 *cometes*

to the eastern Cape, the Transvaal, Rhodesia and Angola. It has been found in a wide range of vegetation types from the margins of forest to the sparse scrub of the Athi Plains. However, it is primarily a species adapted to living in tall grass and secondary scrub. The nests are placed in a variety of situations, at various heights up to about four metres. Nests have been recorded from thatch, between floorboards, under bark, in tree crevices or in vegetation tangles. A favourite nesting site is "Manyara", *Euphorbia tirucalli*. If the nest is in a crevice it fills the space available, but if unconfined it is a coarsely woven globe of rough grasses with a finer lining. If a disused weaver bird's nest is used, this is also lined with chewed grass.

Grammomys are mainly vegetarian but will eat insects as well as green stems, fruit, nuts, flowers and other vegetable matter. Delany's catches (Delany, 1971) suggest that in the scrub forest of Uganda they are found mostly in the branches (28 animals captured above the ground level to 8 on the ground).

Grammomys are entirely nocturnal, lying up in their nests during the day and not venturing out until well after dark. They are solitary except when accompanied by their young.

Their range probably varies with their habitat, but in the optimum conditions of an arable plot in Buganda, Delany found a surprisingly small home-range, consisting of 600—650 sq. metres.

Grammomys are very common in parts of eastern and southeastern Africa but appear to be rarer in western and central Africa. For instance, the density of *Grammomys* in Haut Ituri was found to be only 2.5 per hectare in the best type of environment (marsh edge) and was virtually nil in all other suitable habitats. The only other rodents Misonne caught together with *Grammomys*



in his 200 sq. m plots were *Otomys*, *Lophuromys*, *Dendromus mystacalis* and *Dasymys*. *Oenomys*, the most obvious competitor, was more than six times as numerous. By contrast in a Buganda regenerating scrub forest, Delany caught 41 *Oenomys* to 35 *Grammomys*.

This species is the subject of the famous elephant story that is told to children in so many books. Herbert Lang of the American Congo Expedition repeated what he was told by the Azande, namely that the mice mistake the elephant's trunk for a hollow branch when they are disturbed, whereupon the elephant thrashes about with its trunk, sometimes with fatal results for the elephant. The story could actually have a basis of truth, for several observers have noticed that when this species is disturbed it always seeks to climb upwards, trying to find a crevice to escape into.

Delany (1971) found pregnant *Grammomys* from May to July. He also found evidence that females of this species manage to have more litters than most of the other forest rodents. Placental scars suggested that up to 4 or 5 litters were not unusual, whereas the other species seldom showed evidence of more than one previous litter. From two to five young are born at a time. I have twice disturbed nursing females of this species out of their nests and in spite of a three-metre fall the two or three young were not dislodged from the mother's body and the mother made off with dispatch notwithstanding her clumsy appendages.

Grammomys has become an important experimental animal in malarial research since 1948, when it was discovered to be the natural host of a special malarial plasmodium, *P. berghei*, the vector of infection being a gallery forest mosquito, *Anopheles durenii* (Vincke, 1950). Such a unique self-contained cycle is of course of the greatest interest. The mosquito is a shade and moisture-loving species only breeding in gallery forest streams and rivers. *Grammomys* seems to have a high degree of immunity to this form of malaria and the disease follows a different pattern in this species from that observed in laboratory rats and mice, where it is very virulent and causes death about a fortnight after infection. Other species of wild rodents that were found to be susceptible to this malarial infection were *Pelomys*, *Mastomys*, *Praomys*, *Mus*, *Lophuromys*, *Saccostomus*, *Cricetomys*, *Dendromus*, *Tatera* and *Graphiurus*. Treatment of infected animals with various drugs has been attempted and Chloroquine proved effective.

This is probably only one of numerous small mammal diseases that circulate within more or less self-contained groups of interacting organisms. Its relatedness to human malaria has given it a special importance but there can be little doubt that other cycles of equal interest await discovery.



Rusty-nosed Rat
(*Oenomys hypoxanthus*)

Family
Order
Local names

Ndoga (Kuamba), Ndegwa
(Lubwizi), Empema (Lukonjo),
Nsisa (Lutoro), Bunwe (Lugisu),
Indioro, Nangeti (Luhya)

Muridae
Rodentia

Measurements
head and body

155 (130—180) mm

tail

175 (140—205) mm

hindfoot

32 (29—35) mm

weight

90 (50—121) g

Rusty-nosed Rat (*Oenomys hypoxanthus*)

The red nose of this rat seems to have brought out the whimsy in Thomas, who first described it (1904). A literal translation of its generic name is "wine mouse". The amount of red colouring is very variable, some animals having it only on the nose and rump, while others have the whole body suffused with red. The fur is soft with long guard hairs, the belly fur is white or pinkish with a warm tinge to the margin where it meets the darker dorsal fur.

Oenomys are like *Grammomys* in appearance but their shorter tail and red nose distinguish them. The structure of their teeth is somewhat intermediate between *Thallomys* and *Grammomys*.

The species ranges right across the forest zone of Africa, from Sierra Leone to Kenya, and from Angola to southwestern Tanzania. They are not a



true forest species but are instead typically found in the annual growth that springs up in moist localities or in forest clearings. Such sites can be found in

cultivation, along forest road verges or around telegraph and electricity pylons, along the borders of marshes and, indeed, anywhere within the moist zones where clearing or disturbance encourage fresh herbaceous growth. Montane forests with a broken canopy and dense undergrowth are favourite habitats and the species ranges up to 3,000 m. It seems to like elephant grass, *Pennisetum*, the common weed "namirembe", *Ageratum conyzoides*, and nut grass, *Cyperus*, and I have collected it in each of these common types of vegetation.

The nests are made in a variety of sites, in thick tangles of vegetation well off the ground, on the soil under debris or underground in holes.

The choice of habitat may be due to their relatively specialized diet. Of some 25 stomachs examined over three-quarters contained fresh green matter; leaf shoots, buds, young stems and green seeds probably make up the bulk of their diet. Two stomachs were filled with insects only and caterpillars could be recognized in three stomachs. Their feeding leaves a debris of broken plant fragments.

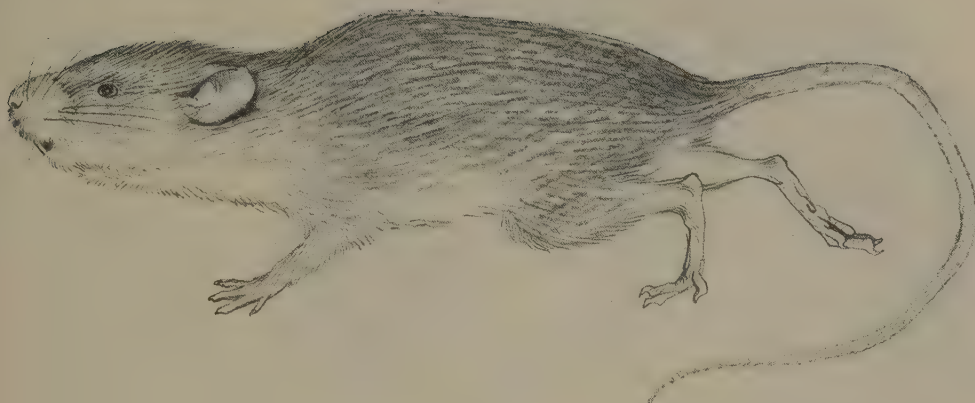
Oenomys have been reported to damage growing millet and rice and they are familiar to most cultivators living in the forest zone. In the northeastern part of what is now Zaire, Emin Pasha was told a story of how the rats' permanently red nose was divine punishment for drinking too much palm oil.

Oenomys are semi-arboreal and can be caught in traps set on branches in bushes and undergrowth. Delany (1971) caught animals up to two metres from the ground. Village boys often capture them as they climb about in vegetation. They are mainly nocturnal but they are also active during the morning and evening. When caught in nests, a single animal, male or female, is the usual catch, unless it is a mother with young. Misonne (1963) established the numbers of *Oenomys* living along the borders of a marsh. This vegetation was dominated by a favourite plant, *Ageratum*, and the density of 17.3 animals per hectare may represent a near optimum for wild conditions although numbers might be higher in some cultivated gardens. In marshland the density of animals fell to 12.5 per hectare but the proportion of this species to other small rodents and insectivores remained about 13½%.

Oenomys have been recovered from the stomachs of several viverrid species, *Genetta*, *Civettictis*, *Herpestes* and *Nandinia* and from the snakes, *Dendroaspis* and *Bitis nasicornis*. On the other hand, only one *Oenomys* was found in 374 owl pellets of *Tyto alba* in West Africa (Heim de Balsac and Lamotte, 1958).

In West Uganda and the eastern Congo (Zaire), *Oenomys* probably breed throughout the year as there are few months without records. Females have 4, 6 or 8 mammae and are slightly smaller than the males. Up to six young can be born at a time but there are usually only three or four. The young soon become miniatures of the parents and are very pretty, rather reminiscent of young squirrels. They are quite adept at climbing.

Opposite, above *Oenomys hypoxanthus*.



THE "SPECIALIST" OR *LOPHUROMYS* DIVISION

The genera in this group are keyed on pp. 502—503 and *Zelotomys* has also been included in the key of the *Rattus* division because of its superficial resemblance with *Praomys* (*Mastomys*).

There is a discussion of the relationship between *Malacomys* and *Colomys* in the murid profile (pp. 570—576).



L. sikapusi

Moist grassy localities

Fur without speckling,
short tail,
reddish belly

H. & B. 130 (120—160) mm
T. 69 (65—85) mm
Hf. 22 (20—23) mm
Wt. 50—101 g

L. flavopunctatus

Moist scrub and forest

Fur speckled,
short tail,
buffy pink belly

H. & B. 124 (100—134) mm
T. 71 (58—94) mm
Hf. 22 (19—23) mm
Wt. 60 (45—95) g

L. woosnami

Montane scrub and forest

Fur, grey brown,
relatively long tail,
brown or yellowish belly

H. & B. 115 (84—127) mm
T. 127 (97—148) mm
Hf. 25 (22—26) mm
Wt. 50 (23—55) g

Local names

Vusu (Kisambaa), Kudi (Kikami),
Kursi (Kikinga), Nguya (Kinyika),
Siku (Lugisu), Jamasiku (Kisebei),
Chamsoget (Kimasai), Liguve,
Lidulu (Luhya), Nyakihuka

(Kihehe), Aduru (Kuamba),
Kinkuli (Lubwizi), Ekisule,
Kisuhura (Lukonjo), Kihukuruzi
(Lutoro), Amuget (Ateso)

Brush-furred Mice (*Lophuromys*)

Species

Lophuromys sikapusi

Lophuromys flavopunctatus

Lophuromys woosnami

Brush-furred mice are distinguished by their dark colouring, peculiarly textured fur and by their short-legged chunky shape. For those familiar with the living animal they are distinguishable by a peculiar smell. These are very successful and common rodents in tropical Africa. There seems to have been a radiation of species in central Africa with numerous forms recorded from eastern Congo (Zaire).

Lophuromys sikapusi has the widest geographic range, *Lophuromys woosnami* the smallest, while *Lophuromys flavopunctatus* is one of the most numerous rodents in the moister areas of East Africa. The commoner species range through a variety of habitats but moisture and grass are probably essential to their existence and so they are not found under closed canopy forest, nor in areas subject to periodic drought. Their success seems to derive from their having specialized in eating insects and particularly ants, an extremely abundant resource in the tropics. Of the "specialized" group of African rodents, *Lophuromys* is the only one that is not restricted ecologically and geographically. In addition to insects, *Lophuromys* also eats frogs, and other small animals, carrion and vegetable matter. Hanney (1964) found that his captives died if their diet was not supplemented by animal matter and a small group of *L. woosnami* kept by me started to cannibalize one another when given a purely vegetarian diet.

Brush-furred mice eat rapidly and the period of time spent actually feeding is very short compared to the vegetarian murids. Delany (1971) found the daily consumption for *L. flavopunctatus* was about 3–4 g a day. Heavily pregnant females however ate 12 g. It is possible that this species is somewhat less insectivorous than *L. sikapusi* and *L. woosnami*.

Olfactory communication would seem to be very important in this genus. The distinctive smell of *Lophuromys* has been mentioned. I have also noticed a grease, presumably of glandular origin, on the fur of a sexually active male *L. woosnami*. This deposit was obvious only at the tips of the dorsal fur and was very concentrated along the bridge of the nose, suggesting that the secretion had been rubbed on. This together with other facets of the behaviour of these insectivorous mice suggests some similarities with shrews.

Brush-furred mice have very variable activity patterns. In general *L. flavopunctatus* is more diurnal, while *L. woosnami* is more nocturnal (Rahm, 1967). However *L. flavopunctatus* is also ecologically variable. In the upper reaches of Ruwenzori, where it is cold at night, this species is exclusively diurnal (see Vol. I, p. 16). In an activity cage in Kampala, Delany found a female was active from midnight to dawn, while a male had short spasms of activity during the morning and also at night.



L. sikapusi.



L. flavopunctatus.

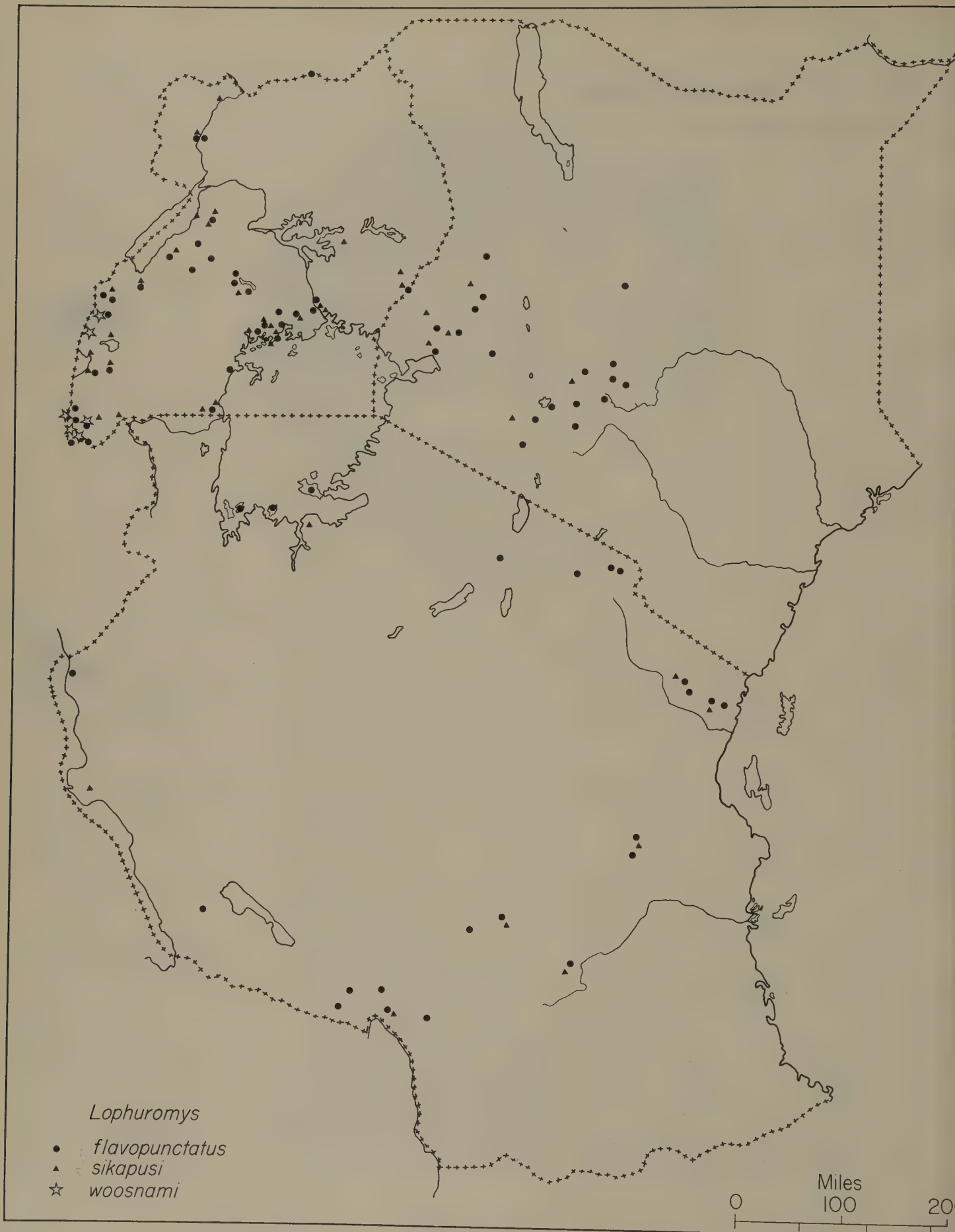


L. woosnami.

Lophuromys

- *flavopunctatus*
- ▲ *sikapusi*
- ☆ *woosnami*

Miles
0 100 200 300
Km.



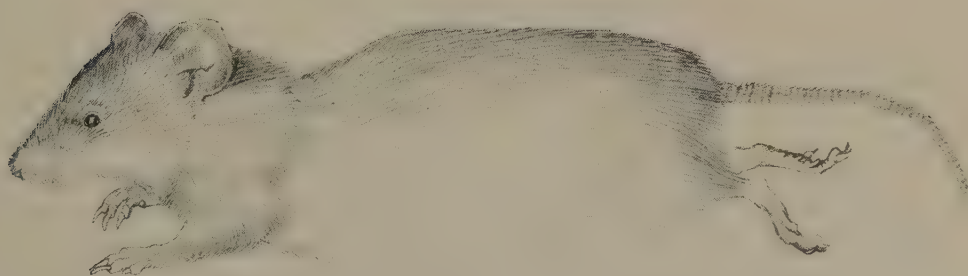
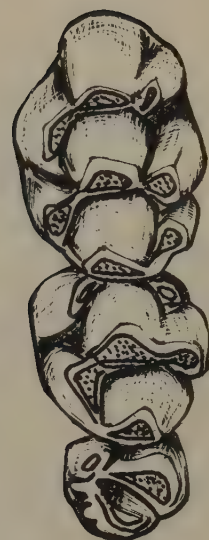
A rough measure of the relative importance of a rodent species can be judged from the proportion they represent of the total small rodents caught in a particular habitat. The figures given by various collectors are very interesting. In the optimum environment of rank herbage within the forest zone, such as parts of the eastern Congo (Zaire) and Uganda the proportion is as high as 35.6% (Rahm, 1967) and 36.8% (Delany, 1971). Where the role of prolific herbivorous species increases, as in the grass savannas of the Haut Ituri, the proportion of *Lophuromys* drops to 12.5% (Misonne, 1963). As habitats grow drier and more prone to fire the proportion drops further. In the Butembo Lubero region Misonne found between 6.8% and 11.6% of *Lophuromys*.

Delany and Kanseriimuhanga (1970) established that *L. flavopunctatus* in a small arable plot near Kampala had a range of about 350 sq. m. Judging from the trapping records, densities in such habitats must be considerably higher than the 14–19 per hectare found by Misonne in the Haut Ituri.

Territorial behaviour has been observed in *Lophuromys* and many collectors have commented on the frequency of torn ears and mutilated tails. These wounds are undoubtedly the result of frequent fights. Delany has not seen females attack other females, otherwise fighting goes on between all classes of animals in captivity.

Nests are made of dry grass and leaves, in crevices, under rocks, roots or fallen timber or in short straight burrows dug by the animal.

The figures given earlier showed that the proportion of brush-furred mice falls where the number of herbivorous rodents increases. It is not known if there is any actual decline in the density of *Lophuromys* or whether these species are in any sense competitive. However Rahm (1967) was surprised to find an apparently suitable locality in the Kivu area (Uvira) where there were no *Lophuromys* at all. He remarks that *Mastomys* (which is an omnivorous species) was present in particularly large numbers. It is possible therefore that this rat is an important competitor. Other factors limiting the species have been discussed, but it is probably a complex interaction of factors that limit *Lophuromys* in the drier habitats. The abundance of food may fluctuate, or loss of cover may increase exposure to predators; physiological factors may also come into play. Disease must certainly play a part. Hanney (1964) found an increase in disease during the wet season and the average of diseased animals was as high as 9% of all the animals investigated.



L. flavopunctatus.



Age class calendar for *L. flavopunctatus* in Mayanja forest (data from Delany, 1971). Spiral line traces hypothetical life span of age classes. Heavy stipple: older animals with worn teeth. Medium stipple: animals with medium tooth wear. Light stipple: young animals with minimal tooth wear.

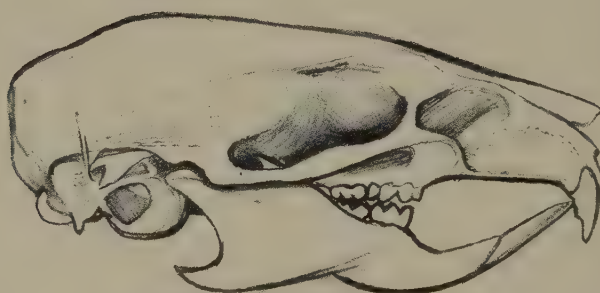
Brush-furred mice sometimes give the appearance of being very delicate. I have shared Delany's experience of finding an undamaged dead *Lophuromys* lying beside one that had been killed in a break-back trap. Delany also saw a young captive that had fallen about 45 cm go into paralysis and spasms but it recovered within a few minutes. They seem to be short-lived; captives may survive up to two years but Delany has estimated the average length of life in the wild at eight months to a year, depending on the season in which the animals were born. The age class calendar opposite traces some temporal age progressions that are extrapolated from Delany's data for Mayanja Forest (1971).

Lophuromys have been retrieved from the stomachs of crested eagles, *Lophaetus*, and they are sometimes numerous in owl pellets. Two captives of mine were killed and partly eaten by a shrew, *Crocidura flavescens*, which managed to get into their cage.

Foresters have thought *Lophuromys* guilty of damaging conifer plantations in Kigezi, but it is more probable that *Otomys* is responsible. *Lophuromys* is easy to trap, whereas *Otomys* is not attracted to bait, hence the probable misidentification of the culprit.

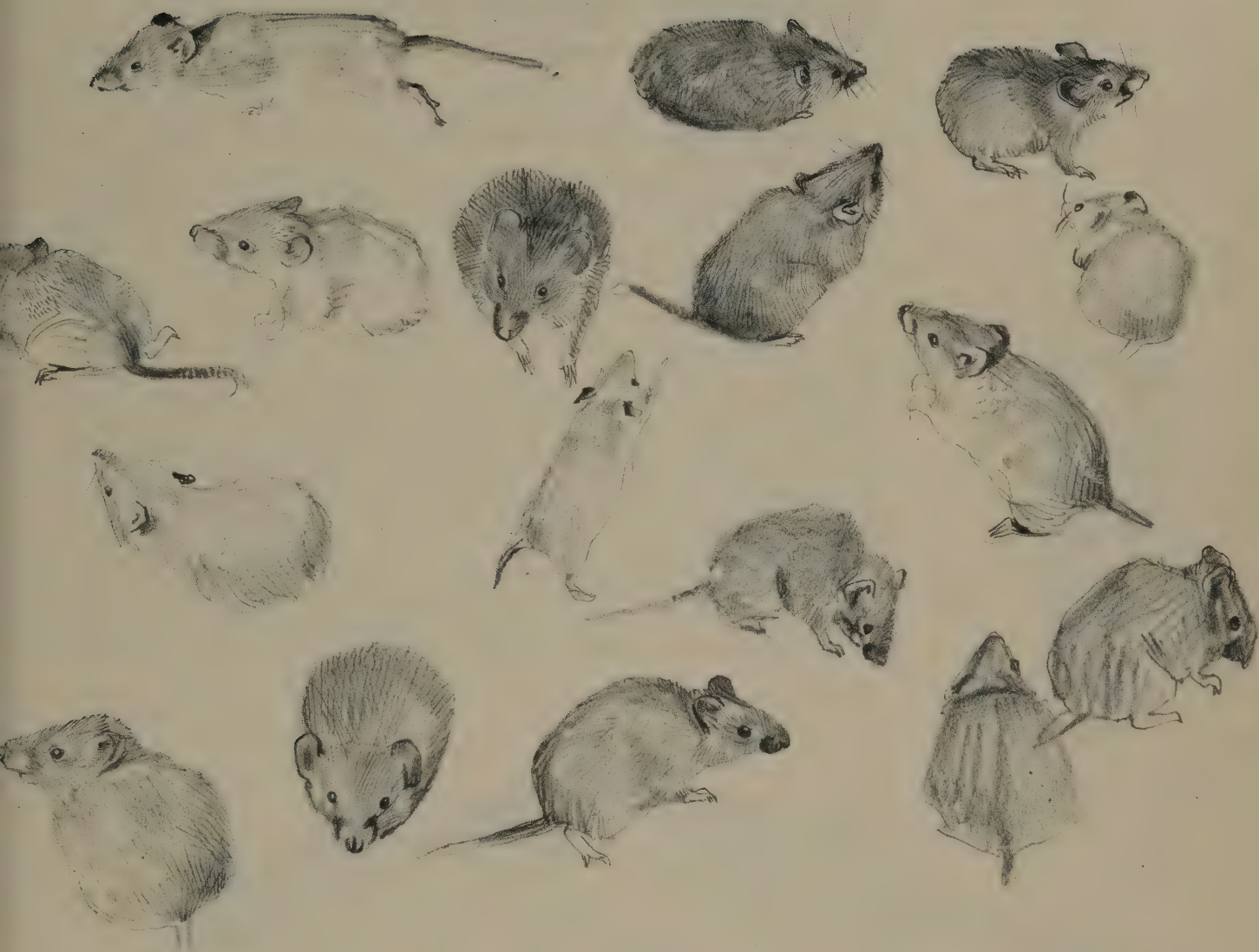
Brush-furred mice have been used as laboratory animals; they are clean, easy to keep and to breed. Rodhain (1934) thought that the variety of different colour forms might provide useful material for genetic study.

L. flavopunctatus has been the subject of numerous studies and its breeding cycles have been shown to be highly plastic and responsive to ecological conditions. In tropical habitats breeding tends to be continuous, particularly where cultivation has diversified the habitat (Rahm, 1967). However, this author found that populations living in forest have biannual breeding peaks from September to December and from March to June. This pattern of breeding coinciding with rainfall peaks appears to be followed by most Uganda populations of this species.



Towards the southern part of its range the influence of rainfall is also apparent in a single prolonged season during the rains (October to May). This pattern can be expected for the southern part of Tanzania.

The gestation period for *L. flavopunctatus* is one month and the young are born with a dark back and covered in fine hair. They weigh between five



and eight grammes. The eyes open and the infant mouse becomes active in four to seven days. By the time it is ten days old it is a miniature of the adults and weighs about twenty-five grammes. At the age of fifteen days the tail has reached an adult length. At one month the young moults its rufous infant coat, a process that is completed in about a week.

Delany (1971) found that larger females have larger litters and that the average number was 2.2 with numbers ranging between one and four. One litter can follow quickly upon another and the extraordinary precocity and speed of development can be appreciated if the brush-furred mouse is compared with other rodents.

L. flavopunctatus.

Uranomys Mouse (*Uranomys ruddi*)

Uranomys is a greyish brown animal with a strong superficial resemblance to the much darker *Lophuromys* species. It has rather similar fur although it has a harsher texture.

This species exhibits a unique condition of the teeth in very young animals. The anterior cusps of the front lower molars are "worn" before there is any chance of friction against the upper molars, showing that tooth "wear", like the acquisition of flat surfaces on the conical teeth of the embryonic dugong, can be genetically pre-determined. This phenomenon which has been described as "l'abrasion prealable" by Heim de Balsac (1967) may involve a peculiar curtailment of development during intra-alveolar genesis or else the cusp tips are resorbed as soon as they are formed. The effect of the cutting away of the cusps is to allow the tubercles behind to grind directly against those of the upper molars as soon as they come into contact. The teeth are also exceptional in having very large pulp cavities in youth but the pulp becomes progressively replaced by dentine, so that an old worn tooth is almost solid ivory.

Uranomys does seem to be a rather strange rodent. It is related to *Acomys*, *Lophuromys* and *Zelotomys* and shares some characteristics with each of these genera. It appears to be closest, however, to *Acomys*.



Uranomys Mouse (*Uranomys ruddi*)

Family Order

Muridae
Rodentia

Measurements head and body

110 (84—134) mm

tail

70 (53—79) mm

hindfoot

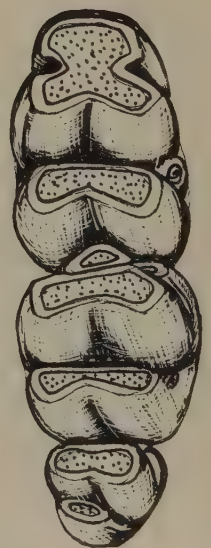
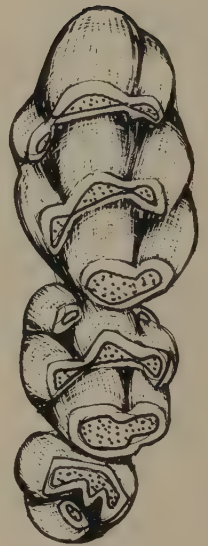
17 (15—19) mm

The overall distribution of this species is very extensive but also very scattered. It will probably turn out to range widely through East Africa but the present records are mostly from Uganda. Other localities are Malawi, the Congo (Zaire) and West Africa.

All records are from grass savanna and secondary savanna. They are usually caught in ones or twos but they have been captured by the hundreds in *Borassus* palm savanna in the Ivory Coast by L. Bellier. This palm generally grows in *Hyparrhenia* grassland and it is interesting that two of the localities where *Uranomys* has been collected in Uganda have communities of this type. Verheyen and Verschuren (1966) dug two specimens out of holes in the Garamba Park but little else is recorded of their micro-habitat.

Heim de Balsac and Lamotte (1958) found seven skulls in the pellets of the West African barn owl, *Tyto alba*, and Bellier found that *Uranomys* in his collecting locality was second only to *Mastomys* (Heim de Balsac, 1967). This very local abundance contrasts with its apparent status elsewhere as a rare and scattered species. They are reported to be mainly insectivorous and nocturnal.

The clearly defined characteristics and ecological niches occupied by the well-known *Acomys* and *Lophuromys* contrast with the apparent lack of definition in the habits and behaviour of the little known *Uranomys*. Is this a relic species not far from the ancestral stock of *Acomys*? Or are its dental peculiarities in any way symptomatic of some unknown specialization? However, until more is known of its habits this species remains an enigma and further data on its ecology and behaviour would be most interesting.



KEY TO ACOMYS

Description

Measurements

Species

Relatively long tail and hindfoot, grizzled brown back, fulvous sides and face, soft white belly fur and cheeks.

Zygomatic arches with parallel sides.

Rocky country species

H. & B. 98—120 mm

T. 72—97 mm

Hf. 15—16 mm

Skull 25—27 mm

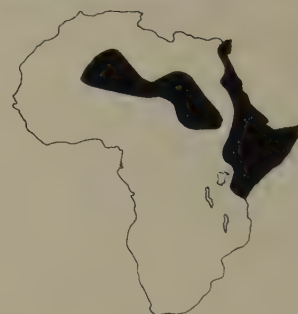
Acomys dimidiatus

racies:

A. d. hystrella

A. d. ignitus

(includes *montanus* and *intermedius*)



Uniform grey brown back and sides with dirty white belly.

Zygomatic arches with bowed sides.

Arid semi-desert species

H. & B. 74—94 mm

T. 48—84 mm

Hf. 14—15 mm

Skull 25—26.6 mm

Wt. 11—33 g

Acomys cahirinus

racies:

A. c. kempi

(includes *percivali* and *pulchellus*)



Dark brownish back. Sides of head and body reddish, long-nosed, nasals over 9.8. Dry woodland species in rocky sites

H. & B. 90—109 mm

T. 80—100 mm

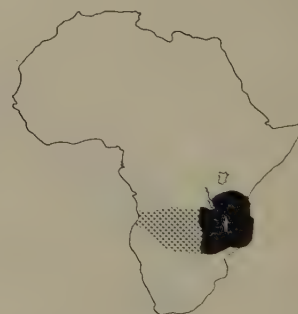
Hf. 16—18 mm

Skull 23.5—24.9 mm

Acomys spinosissimus

racies:

A. s. selousi



Relatively short tail and hindfoot. Spines extending up to ears. Speckled back, relatively short-nosed, nasals 9.5 or less.

Dry savanna species in grassy situations

H. & B. 83—96 mm

T. 42—48 mm

Hf. 12—15 mm

Skull 23.5—24.9 mm

Wt. 19—27 g

Acomys subspinosus

racies:

A. s. enid

A. s. nubilus

A. s. wilsoni



Spiny Mice (*Acomys*)

Species

Acomys dimidiatus

Acomys cahirinus

Acomys spinosissimus

Acomys subspinosus

Local names

Mgona chekede (Kipokomo),
Nachiri, Kukwai (Karamojong)

Spiny mice are immediately recognizable by the thick spiny hair growing on the back. They are found over most of the drier parts of Africa as well as the Middle East and North-west India.



A. cahirinus.

The different niches occupied by the four species represented in East Africa are briefly indicated in the key. All of them depend upon shelter, which they may find in rocky crevices, cracked soil, gerbil and other rodent burrows or in the chambers of termitaries, according to their habitat. In Egypt a type of *Acomys cahirinus* has become a commensal of man and occupies the house-mouse niche. Curiously enough this variety has lost the white belly that is characteristic of all other *Acomys* species. Darkening of the belly is also found in other commensal mice of the *Mus* and *Praomys* genera.

Spiny mice are opportunistic feeders and can even survive on coarse dry plants. They eat grass seeds, leaves, dropped grain, nuts, flowers and various animal matter. Vesey-FitzGerald (1966) found *A. s. selousi* eating beetles, bugs, ants, termites, millipedes, spiders and small snails as well as seeds. He found the remains of these foods accumulated together with dung in middens, where the animals obviously took their food to eat under shelter. They have been observed feeding on the waste of *Rousettus aegyptiacus* inside an Egyptian

tomb. Watson (1950) reports that in Karamoja spiny mice are accused of climbing maize stems to get at the cob.

Spiny mice are primarily nocturnal but some species are active during the early morning and in the evening. They are terrestrial but have been trapped in trees. They are gregarious and their general behaviour suggests that, apart from their adaptation to arid habitats and the acquisition of a spiny cape, they are relatively generalized mice resembling the genus *Mus*. The spines presumably developed to deter predators, the easy shedding of the tail is probably another device for escaping enemies. I am unaware of any experimental



investigation into the deterrent effect of the spines, but domestic cats seem to find these mice difficult to eat.

Their reproductive behaviour has been the subject of several interesting papers by Dieterlen who has kept various species of *Acomys*. He found that they bred continuously in captivity. Periods of food shortage might restrict





breeding in the wild but under good conditions wild spiny mice probably breed over the greater part of the year. Remarkable recruitments of numbers are possible in spite of the litters being small. Dieterlen bred 179 animals from a stock of seven and established that the gestation is peculiarly long, being 5—6 weeks instead of 3—4 as it is in most other mice. Watching many births of *A. cahirinus* he observed unusual social behaviour amongst the females. Females that had already given birth very frequently assist the parturition, serving as “midwives” by biting the umbilical cord and licking and cleaning the new-born while the mother delivers the rest of the litter.

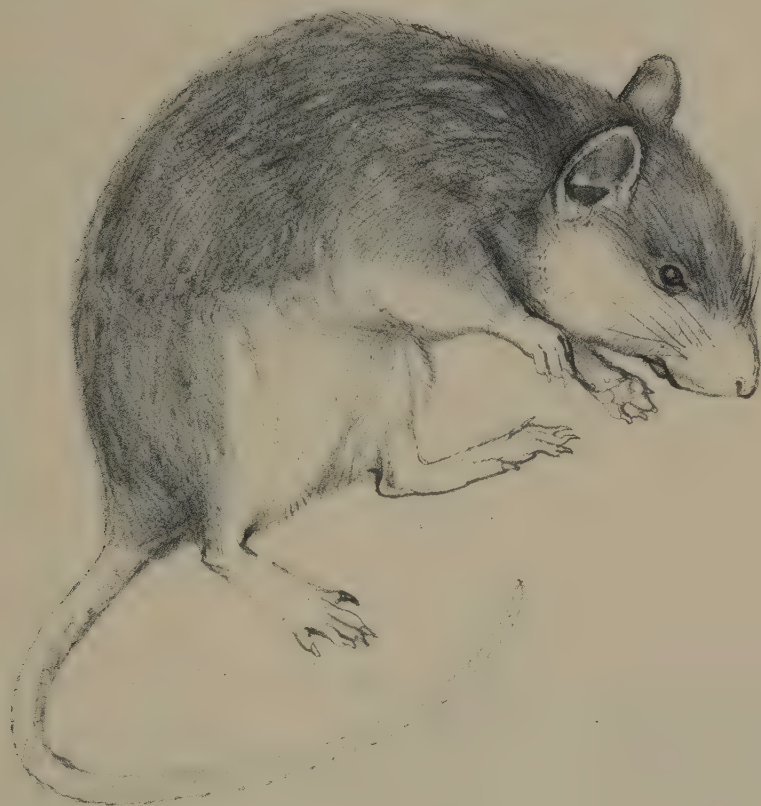
Acomys dimidiatus gives birth to slightly less developed young than *A. cahirinus*, but after a few days all young *Acomys* are running about. The very rudimentary nests of spiny mice and the length of their gestation are probably connected with the unusual precocity of their young and “mid-wifery” is probably important to the mother mouse, whose young may weigh 5 or 6 grammes at birth.

Females have 4 or 6 mammae and wean their young at two weeks. The young grow rapidly and are sexually mature at 2 to 3 months. Females have one litter after another in captivity, the younger ones bearing small litters, while the older ones have up to five young at a time.

Acomys are popular as pets and are easily kept and bred in the laboratory.

Broad-headed Mouse (*Zelotomys hildegardeae*)

Zelotomys is superficially very like *Praomys*, with soft grey-brown fur. Its tail is generally white or whitish in colour and shorter than the body. The broad skull tends to be subject to much individual variation. The incisors are generally very pro-odont and protuberant and the molars have prominent cusps.



**Broad-headed
Mouse**
(*Zelotomys
hildegardeae*)

**Family
Order**

Muridae
Rodentia

**Measurements
head and body**

115—137 mm

tail

86—115 mm

hindfoot

20—25 mm

weight

56—64 g



Zelotomys belongs to a group of “omnivorous specialists” and is related to *Uranomys*, *Malacomys* and *Colomys*.

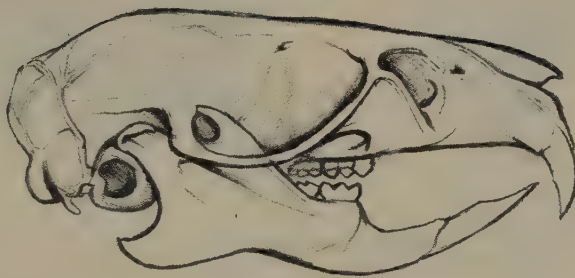
Z. hildegardeae seems to be widely distributed in the East African “overlap” region (see Vol. I, pp. 8, 80) from eastern Zaire (Congo) to Malawi, Zambia and Angola. One other very localized species, *Z. woosnami*, is known from South-west Africa.

In Uganda and eastern Zaire most specimens have been caught in clumps of sword grass, *Imperata cylindrica*. The species as a whole seems to belong to moist, grassy savannas and scrub.

Zelotomys is insectivorous and likes myriapods and dung beetles. The average food capacity is recorded by Delany (1964b) as about 4 cc. The animal probably forages for most of its food under the grass cover, and the scarcity of insects during the dry season plus the hazards of fire and predators must tend to keep the density of *Zelotomys* fairly low. In *Imperata* grassland with very sparse bush, *Zelotomys* represented 2.15% of the total number of small rodents caught in the Queen Elizabeth Park.

Like shrews these rodents may rely upon offensive smell to protect themselves from mammalian enemies. Rood (personal communication) found the odour of a captive so unpleasant that he kept the animal away from his house. Subsequently a house snake, *Boaldon*, managed to enter the cage and swallowed the mouse.

One pregnant female has been recorded for November in southern Kenya, and one for July in western Uganda. Five to seven young are born and the females have ten mammae.





**Velvet Rat,
Colomys Rat
(*Colomys goslingi*)**

**Family
Order**

Muridae
Rodentia

**Measurements
head and body**

123 (117—140) mm

tail

161 (145—180) mm

hindfoot

38 (35—39) mm

weight

65 (50—75) g

Velvet Rat, *Colomys* Rat (*Colomys goslingi*)

Colomys is easily recognizable by its dramatically contrasting chocolate and white velvet fur (which is completely waterproof). Its swollen bulbous nose, armed with numerous stiff vibrissae is somewhat reminiscent of an otter or potamogale. This is a semi-aquatic rat and its broad hind feet are well adapted to rapid swimming.

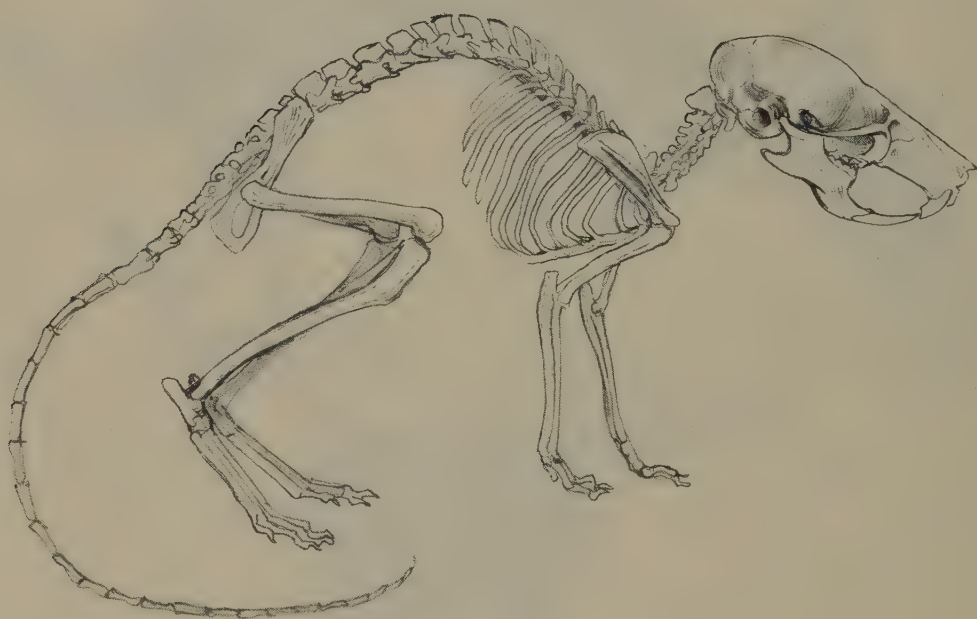
A quarternary fossil attributed to *Colomys* has been described from Serengeti (Dietrich, 1942). The genus seems to have a rather scattered distribution today, which may be partly due to inadequate collecting but may also be a reflection of climatic vicissitudes in the recent past.



Colomys have been found in swamps and rivers in forest country, at both high and low altitudes in the Cameroons, in Angola, in eastern Zaire (Congo), on the Mau in Kenya and it is recorded from Ethiopia.

The habitat of this rat is thickly vegetated swamp and muddy rivers. I have trapped it along forest streams in Bwamba, in western Uganda, where the principal plants are a dense growth of Zinziberaceae, Marantaceae, *Phoenix reclinata* and ratten palms, *Calamus*. All the animals were trapped on the water's edge or on muddy islands in the swamp. The habitat is prone to seasonal flash floods. Rahm (1967) found a nest, consisting of a few dry leaves at the end of a short burrow about 30 cm long.

Colomys feed mostly on aquatic insects, worms, slugs, crustaceans and also on a certain amount of vegetable matter. They can be trapped using either fish or vegetable baits, and I maintained a captive in good health on a diet that was principally maize meal or brown bread with occasional insects, worms, slugs and snails. At Elburgon (altitude 2,450 m) an animal was trapped in a forest camp as it explored a sack of flour.



I have watched *Colomys* searching for food in watery mud; the animal wades through the water raising itself as high as it can on its toes. While the forelegs are occupied sifting mud and debris, the hindlegs are sometimes placed very wide apart to achieve balance. The nose is held close to the water's surface with the vibrissae spread out so that they are in contact with the water; presumably they assist in the detection of prey disturbed by the sifting hands. A quick pounce marks a capture and the prey may then be taken to a drier spot. When the object is a worm, the rat works it vigorously through the hands pushing the body contents down the length of the worm as it swallows it head first. The animal's whiskers are the object of constant grooming and there can be little doubt that the peculiar muzzle and vibrissae are an important specialization.

There is an interesting modification of the muzzle of *Colomys* in relation to the incisors. A comparison can be made with the relatively conventional rodent muzzle of the related *Malacomys*. In the latter, the long straight vibrissae grow in the area of the muzzle lying between the nostrils and the eyes, while the upper lip slopes sharply away from the nose to allow maximum exposure of the incisors; indeed *Malacomys*, like many other rodents, is incapable of "closing its mouth". In *Colomys*, this upper lip is greatly swollen to accommodate the roots of curved white vibrissae which fan out to surround



Colomys,



Malacomys.

the mouth, the chin too, carries well-developed hairs and is also relatively swollen. *Colomys* is actually able to "close its mouth", the two halves of the upper lip meeting the lower and sealing over the teeth. This modification might have something to do with its method of seeking food and its semi-aquatic life.

Colomys is very buoyant, swimming very rapidly with powerful thrusts of the hindlegs. The animal lies high in the water with the water-line more or less coinciding with the sharp demarcation between its dark back and white belly. The animal generally grooms itself on emerging from the water. In addition to swimming well *Colomys* is capable of sudden long jumps and is an agile climber.

The *Colomys* that I kept for some months was very quiet and tame from the start. Its cage needed cleaning daily as its dung was rather liquid and foul smelling but apparently healthy. It was mainly nocturnal, but there was generally some activity in the morning and evening as well. One that was brought to me in Bwamba had just been killed at 9 a.m., having been seen in swampy vegetation besides the road. Trapped specimens have all been taken at night.

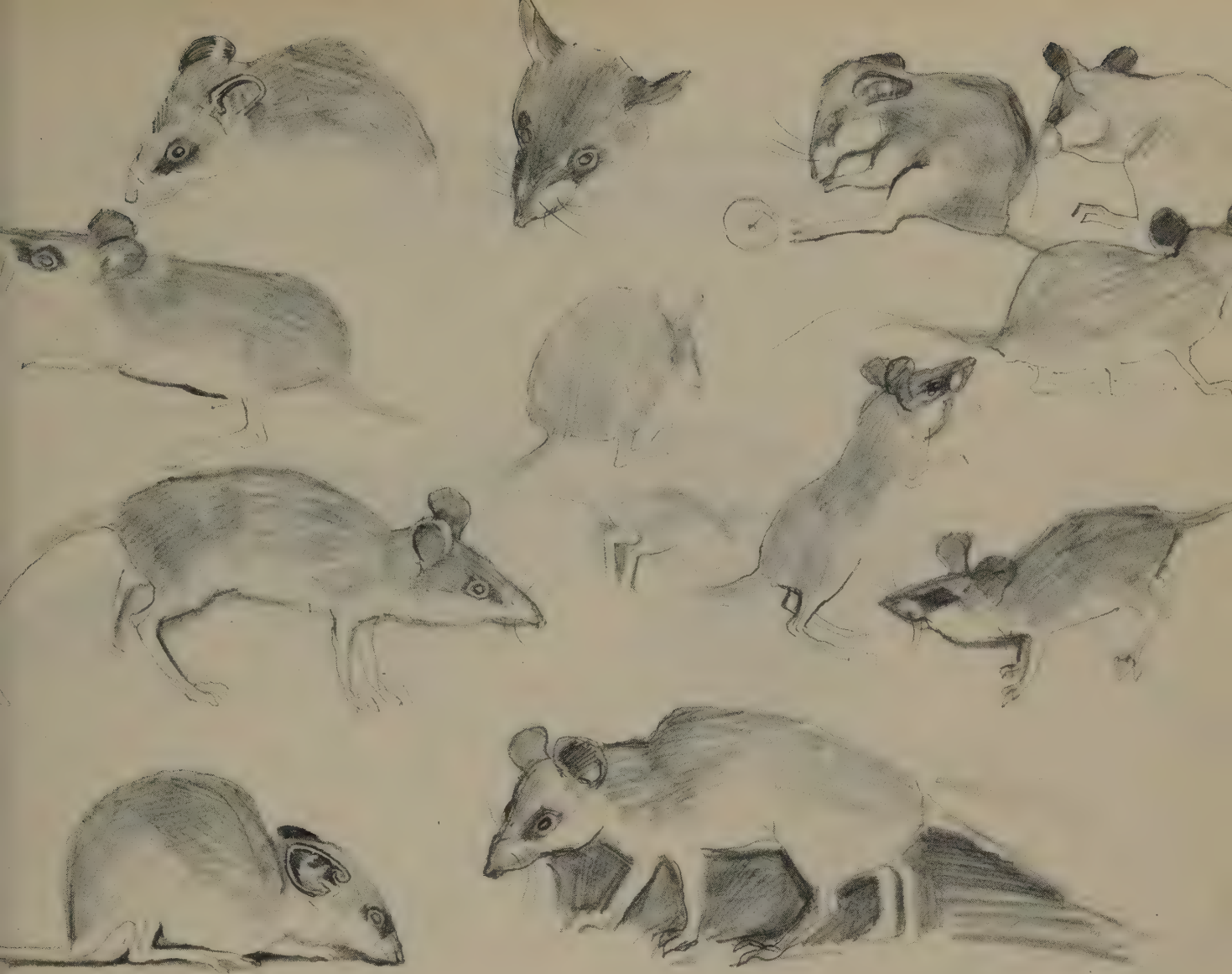
They are probably solitary animals but I captured three adult males all in breeding condition with a single string of traps in one night. Although the individuals were well spaced there is little doubt that contact between them could easily have been achieved. One of these animals was heavily parasitized with intestinal worms; the others were not.



Colomys has been retrieved from a buzzard's crop and is probably eaten to some extent by snakes and the marsh mongoose, *Atilax*, which are common in their habitat.

The sexually active males develop a glandular secretion which stains their chest a yellowish colour and makes the fur distinctly greasy.

At least one breeding season or peak can be suggested for western Uganda and eastern Congo (Zaire) with records of sexually active males in March, a pregnancy in April, and four records of young and one lactating female in June—July. Hayman captured a male and female in the same trap during March in the Semliki Valley and he caught a half grown young in the same locality the following night.



**Long-footed Rat,
Malacomys Rat
(*Malacomys longipes*)**

**Family
Order**

Muridae
Rodentia

**Measurements
head and body**

166 (135—178) mm

tail

180 (156—208) mm

hindfoot

41 (35—44) mm

weight

90 (50—145) g

Long-footed Rat, Malacomys Rat (*Malacomys longipes*)



Race

Malacomys longipes centralis

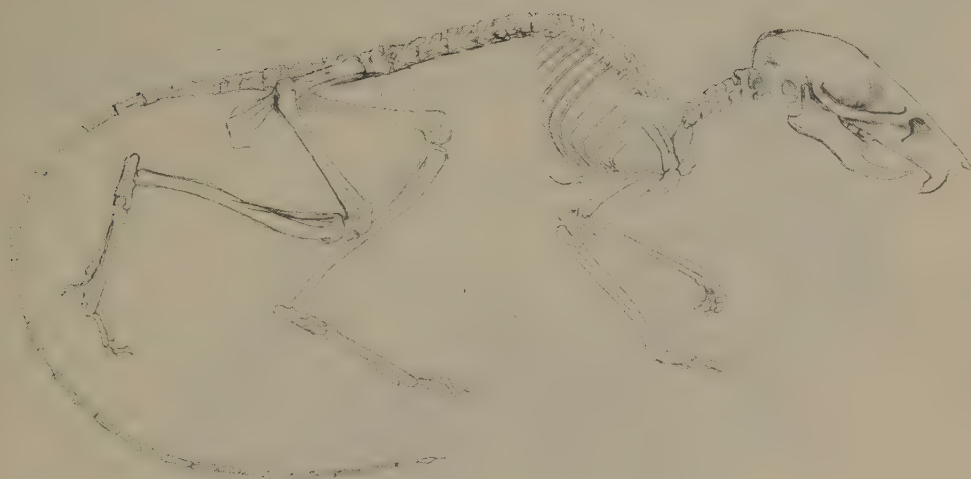
Malacomys is a dark brown soft-furred rat with very long hindlegs and forearms. The colouring is rather variable and an irregular moult pattern may mark the animal with very dark patches on paler brown, sometimes with reddish areas around the rump and ears. The belly fur is made up of slaty hairs with white tips, giving a pale grey effect. The ears are round and large and the whiskers are very long. Size and weight are rather variable.

Malacomys longipes is found from West Africa to the Victoria Nile within the forest zone. Two sympatric forms are found in Ghana, a situation that has been discussed in the profile of Murids.

Malacomys is a forest species, only found near water under dense cover and on soft wet soils with plenty of leaf litter. In restricted areas of wet, heavily shaded forest (often characterized by abundant wild ginger, Zingiberaceae, and wild arrowroot, Marantaceae, species) *Malacomys* is sufficiently common to be a dominant rodent species. It makes grass or leaf nests

in natural crevices or among tree roots; these sites are sometimes relatively exposed.

Their diet is rather interesting as they seem to choose both vegetable and animal foods in nearly equal proportions. Out of 30 stomachs (including 11 recorded by Hatt, 1940), 15 contained a mixture of animal and vegetable matter, 11 contained vegetable alone and 6 contained animal matter only. Fallen fruits, seeds, nuts and roots appear to be the principal vegetable foods. Termites, crickets, slugs, snails, caterpillars, crabs and a toad are recorded animal foods. An adult male confined in a small cage with a pregnant female killed and partly ate her but this cannibalism may have been induced by the stress of capture and travel.



Food is held down by the forepaws and gnawed. Slugs are eaten after a great deal of biting and pummeling by the forepaws, which releases a lot of messy slime that tends to collect on the paws and lips. Once the slug has been eaten the rat chews any fibrous humus or vegetation it can find pulling the fibres out of the mouth and teasing them through the hands, until all the slime has been rubbed off on the debris. Snails are dealt with in similar fashion but are gnawed down from the rim. Feeding is generally followed by prolonged grooming and bathing sessions. All my captives have dabbled in water and drunk frequently.

Malacomys has a rather similar gait to *Deomys* and *Scutisorex*, trotting on its toes with the body held well clear of the ground. It is also a careful but capable climber through tangled vegetation.

Malacomys are nocturnal, but captives tend to be intermittently active throughout the day. Delany (1971) charted the activity of a captive over 24 hours and found the principal feeding period was during the first three hours of darkness, but the animal was most active in the last three hours of the night.

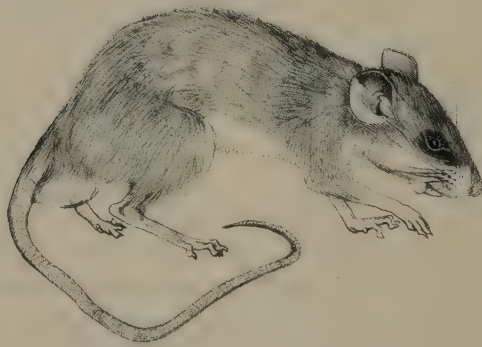
These animals are more or less solitary, but I have captured three animals together in the same trap: an adult male that was not in breeding condition, a



pregnant female and a juvenile. Two other traps nearby caught two more animals on the same night, so that the density of individuals in the area was clearly very high. It is possible that small family associations are maintained, even when animals are not in breeding condition.

Malacomys shares its habitat with several other rodents. The omnivorous *Praomys* must be an important competitor at the drier end of the forest floor catena and *Colomys*, when it is present, probably replaces *Malacomys* in the wettest habitats. *Scutisorex* is presumably entirely insectivorous but it has a similar niche and is very much rarer than *Malacomys*, and might actually suffer from its competition. However the most ecological overlap is with *Deomys*. This cricetine rodent might have filled the swamp forest niche long before the evolution of the murine *Malacomys*. Evidence for its decline in competition with *Malacomys* is to be found in the ancient and isolated forest at Sango Bay, where the latter rodent is absent. Figures comparing the relative status of *Deomys* in Sango Bay and in Bwamba Forest are shown in the profile of that species.

Malacomys have a mild disposition and are not difficult to keep in captivity. There is no clearly defined birth season, but it is possible that there are peaks of breeding activity.



Dormice

GLIROIDEA

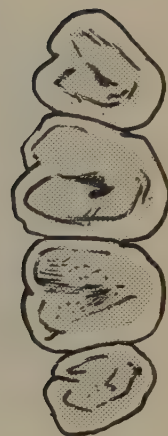
Muscardinidae

The dormice are distinguished by the structure of the zygomatic process and by their teeth.

The superfamily is one of the three subdivisions of the Myomorpha. Unlike the Muroidea, this group has not radiated into a vast number of forms but has remained rather generalized.

Most dormice are arboreal, have bushy tails and are omnivorous.

They range over most of Eurasia and Africa, where a small number of species successfully fill a niche which seems to lie between that of the squirrels and that of the arboreal mice.





African Dormouse
(*Graphiurus murinus*)

Family Muscardinidae
Order Rodentia

Local names

Panya miti (Kiswahili), Neki
(Kipokomo), Funde (Kigogo),
Mderi (Kihehe), U'lungera
(Kikinga), Isene (Lugisu),
Kererut (Kimasai), Chizuguzu
(Luhya), Asiring (Itesot), Nalwado
(Karamojong), Anjarange
(Kuamba), Ka'una (Lubwizi),
Embutu (Lukonjo)

Measurements
head and body

75—105 mm

tail

58—95 mm

hindfoot

13—18 mm

weight

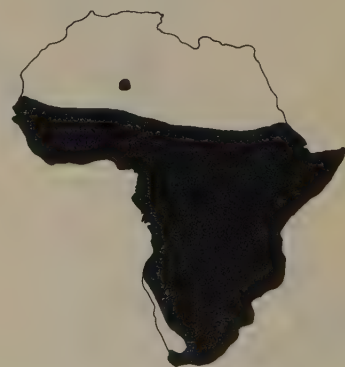
18—30 g

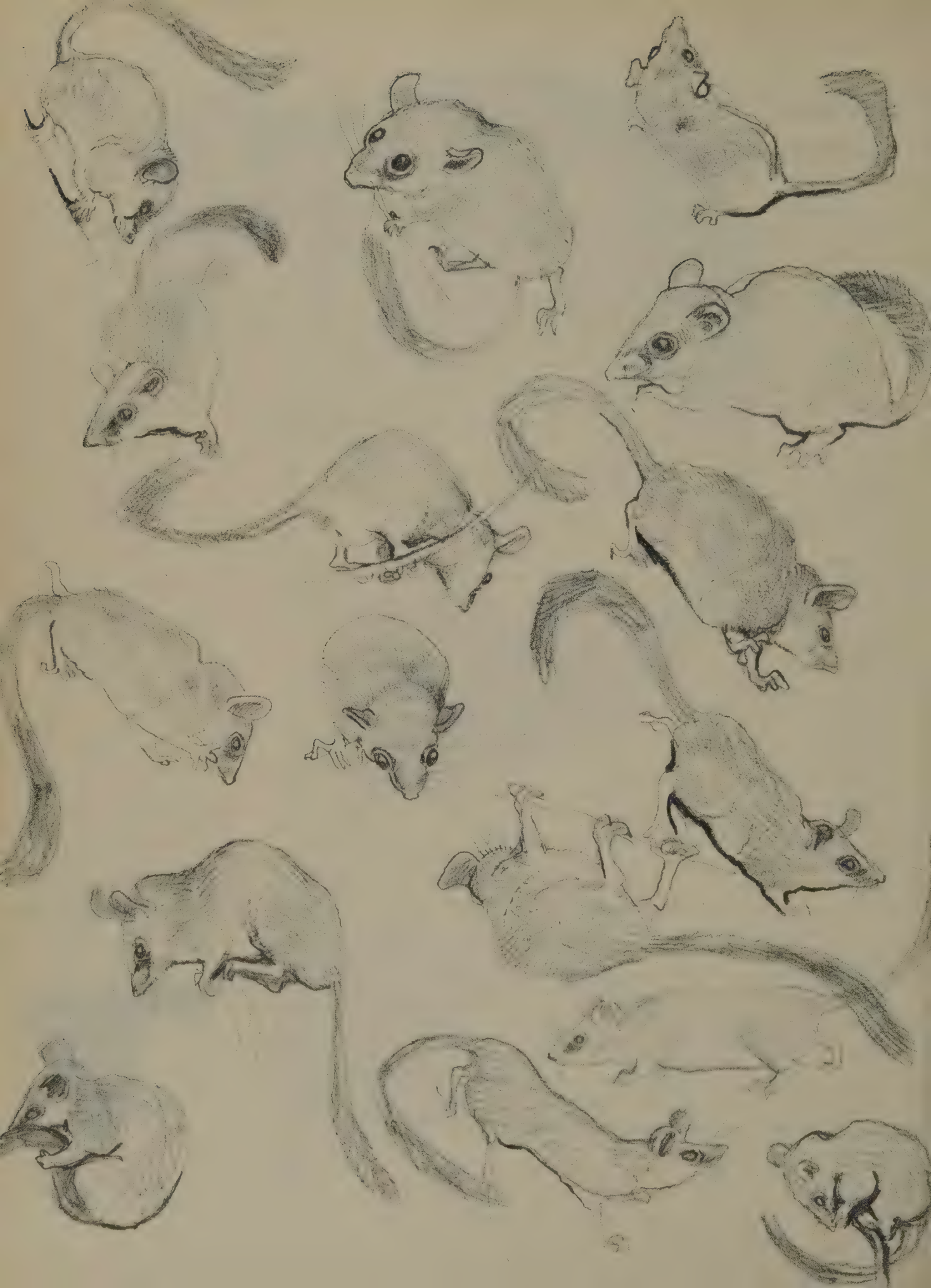
African Dormouse (*Graphiurus murinus*)

It is possible that more than one species of dormouse occurs in East Africa, but among some eighteen forms described from this region there is a great deal of synonymy and many forms have been described on the basis of colour, a very variable factor in this genus. Indeed, not only is colour variable but these animals also stain themselves with an insect "cochineal," which derives from earwigs, common inhabitants of dormice nests (Hatt, 1940). I have noticed this reddish stain on the head and chest of a dormouse from Uganda and other naturalists have also found this staining.

Dormice are generally tawny-grey in colour, with younger animals tending to be greyer and older animals more tawny. The pale underside contrasts more sharply and the pattern on the face or tail may be more or less contrasting in some populations. Enumeration of the many named races seems pointless for, as might be expected, the animals from moist, forested areas tend to be darker, i.e. *G. m. saturatus* from western Kenya and Mt Elgon. A paler form, *G. m. griseus* comes from semi-arid northern Kenya.

The African dormouse is distributed over most of the continent south of the Sahara and the species is extraordinarily adaptable where habitat is concerned. Dormice live in woody vegetation in some very dry, hot habitats and also in cold mountain forests and in all types of savanna. They are common in cultivated areas and are a familiar commensal in houses and huts, where they generally live in the roof or in the thatch. Their round nests are made with any available local material, leaves, grass, shredded bark, feathers, cotton, cloth or paper, and can, it seems, be situated anywhere; they have been found in forks of shrubs, various holes, crevices and hollows, in swallows' nests, hollow coconuts and, very commonly, in bunches of bananas on the tree and in beehives. Stored food, usually nuts or small unripe fruits, is sometimes found in the nest. Their diet is very catholic but they have some well-known feeding habits. Bird flesh is a very effective bait for trapping them. They will also smell out freshly killed birds in the trees, in a house or in camp and are a pest to bird fanciers with aviaries and to collectors in the field because of this propensity for finding birds. Eggs and nestlings are also eaten, and there can be little doubt that they kill sleeping birds at night. Their incredible speed and agility in the branches and their razor-sharp, pointed incisors must assist this predatory role. They are sometimes visible at night when they catch insects attracted to the light. Their hunting technique consists of a lightning rush towards their prey, whether bird or insect, which is promptly seized by the head. When captive dormice are given a bird, a small mouse or a lizard, the brain is usually eaten first. They may sometimes be seen on leaf litter under the trees, where they probably eat termites. Honey gatherers from many parts of East Africa complain that this animal is a very common tenant of beehives, nesting in corners of occupied, as well as empty, hives. They feed on the bodies of the dead bees and probably also on honey and wax. Duff-MacKay (1965) reports watching a honey gatherer opening a hive in Kenya





"The hive was heavily infested with wax moth, *Galleria mellonella* Linnaeus. Amid angry bees the man removed handful after handful of the caterpillar's silk, mixed with bits of broken comb, and at last brought out to my surprise a dormouse, *Graphiurus murinus* (Desmarest). The dormouse itself was an amazing sight, being quite incredibly fat. I later measured the layer of subcutaneous fat in the lower abdomen and found it to be 8 mm deep, beside which there was a large volume of fat surrounding the viscera. The stomach contained a brown sludge with fine white specks in it—presumably honey and wax. . . . On questioning the man, he told me that *Galleria* and *Graphiurus* invariably occur together in infected hives. . . . One wonders however, whether there is a true association between the presence of *Galleria* and of *Graphiurus* in these hives, and if so, what is the nature of this association. Could it be that the making of a relatively large hole into the hive through the bung (gnawed by the dormouse) leaves a convenient unguarded entrance for the moth?"

Altogether the association of *Graphiurus* with insect communities might be a very interesting field of study, for it was mentioned earlier that the staining of some individuals was thought to be due to earwigs. Chapin (in Hatt, 1940) describes a nest

"One old double (swallow's) nest was especially interesting by reason of its strange occupants. It was attached to the undersurface of a rock, a little rough, it is true, but nearly horizontal. Both compartments were provided with round entrances but they were also connected within by a small aperture. A female dormouse had taken possession of the left-hand nest and stuffed it with dry vegetable material, and was now living there with her three well-grown young. But the outer entrance of her side was closed by the nesting material, the dormouse evidently passing in and out through the right-hand chamber, where their way was almost barred by a nest of a large species of paper wasp. Still more remarkable, the space between the top of the dormouse nest and their stone ceiling was crammed with several hundred earwigs, light brown in colour and bearing pincers—very long in some individuals—on their caudal extremities".

The dormouse is nocturnal but is occasionally active during the day when sunlight is not too strong. It has rat-like eyes and large naked ears and seems to have quite acute vision and hearing. It is able to detect by smell choice foods in box traps so its sense of smell must also be quite well developed. Dormice are extremely agile climbers running up and down stems with equal ease. They can balance on very thin branches as on a trapeze, or run down hanging upside down. The feet have well-developed pads and also sharp little claws. Eibl-Eibesfeldt (1958) reports that dormice can climb on twigs even after amputation of the claws, using the pads for a firm grip.

On trips to Bwamba in West Uganda at different times of the year, I invited small boys to bring in animals. In March quantities of dormice were brought along, mostly females with young. In July no dormice were brought. In October, November and December, dormice of both sexes were brought in, some of the females being in breeding condition. The disappearance of dormice in July might be due to chance, but if the making of conspicuous nests is related to breeding seasons, it could be of some significance.

Very little is known of the social life and behaviour of this species and it would be worthwhile investigating.

They have been shown to become lethargic when experimentally transferred from a high to a low temperature (Lachiver and Petter, 1969). This

capacity could be an advantage in some habitats but it is difficult to see its usefulness in others, although it might serve to increase the ecological plasticity of the species.

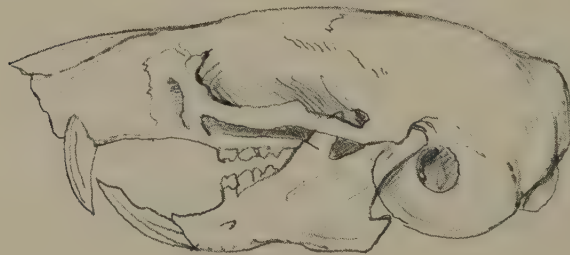
In the past the dormouse was a familiar occupant of huts but the invasion of East Africa by the black rat, *Rattus rattus*, has displaced it in many localities.

Young dormice are common pets of children in Africa although they tend to bite when adult. In captivity, *Graphiurus* shows signs of strong territoriality; captive males have been known to kill and eat one another. In the wild, however, males and females have been found to share a nest with the young. However, as many as eleven adults of both sexes have been found in one nest. They make various twitters and a surprisingly loud raucous shriek.

Breeding records do not provide conclusive evidence of breeding seasons but there appear to be breeding peaks. In western Uganda numerous pregnant and lactating females have been recorded in March and one pregnant female in October. Three pregnancies have been recorded from Mt Umengo in Kenya for November, and two from Mt Elgon also for November. In South-west Tanzania, a pregnant female was caught in January and a juvenile in March. Gestation is probably in the region of 24 days.

The female has 6 to 8 mammae and can feed 1 to 5 young. In a litter of two, I found the young weighing $3\frac{1}{2}$ g each at birth and measuring 40 mm—head and body—with an 18-mm tail. The tail seems to grow faster than the body and is very easily damaged. If the tip is broken off, the tail grows a broad brush of hair. (The two detailed drawings portray animals with undamaged (p. 672) and regenerating (p. 669) tails.) As in lizards, the shedding of the tail would appear to give the animal an advantage in escaping from predators. Regeneration of a vertebra has been observed in European dormice as well as the regeneration of a disk between the vertebrae.

Young dormice grow rapidly and twitter shrilly. European dormice build their first nest at the age of 55 days.



Dormous *Graphiurus*.

Hystricomorphs

Hystricomorpha

The largest contemporary rodents belong to this suborder which includes the South American capybara, *Hydrochoerus*, which weighs up to 50 kg, the guinea pig, *Cavia*, and the coypu, *Myocastor*. The two latter species are feral in parts of East Africa: *Cavia* rather precariously near the veterinary station at Mpwapwa, and the coypu near Mt Kenya and on the Aberdare Mountains.

The hystricomorphs present an unsolved zoogeographical puzzle because there are striking resemblances between the African and American porcupines and several South American rodents and the African *Thryonomys*.

Hystricomorphs have a greatly enlarged infraorbital foramen, which contains the deeper part of the masseter. This arrangement of the chewing musculature distinguishes the suborder.



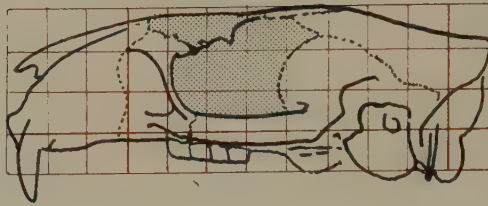
Hystric (Africa).



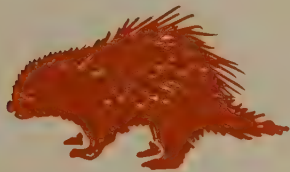
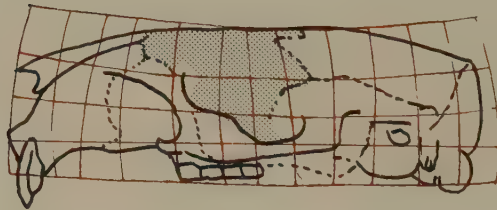
Coendu (South America).



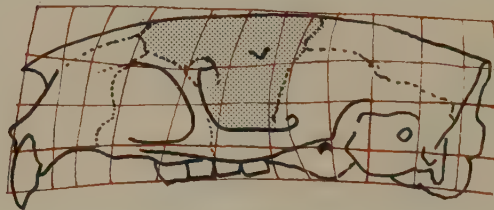
Trichys (Malaysia).



Atherurus (Africa).



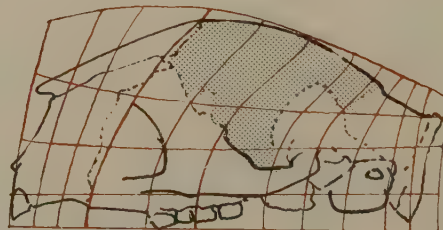
Thecurus (Indonesia).



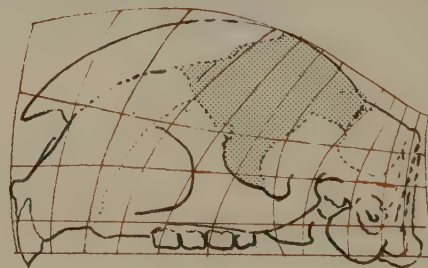
Hystrix brachyurus (India).



Hystrix africae-australis.



Hystrix cristata (Africa).



Old World Porcupines

Histricidae Atherurinae Hystriinae

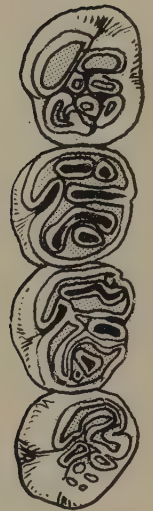
The old world porcupines range across tropical Asia to Africa. They include two distinct subfamilies, the smaller, less spiny, brush-tailed porcupines and the very highly evolved and familiar crested porcupines.

The Atherurinae are forest animals dispersed over numerous islands of the Oriental region and in the African tropics. This distribution demonstrates their ancient and conservative status, because the last forest connections between the continents were no later than the mid-Miocene. Savanna connections are more recent, however, and the more adaptable *Hystrix* is found over a much wider range in Africa and Eurasia and has found its way to some of the Indonesian islands as well.

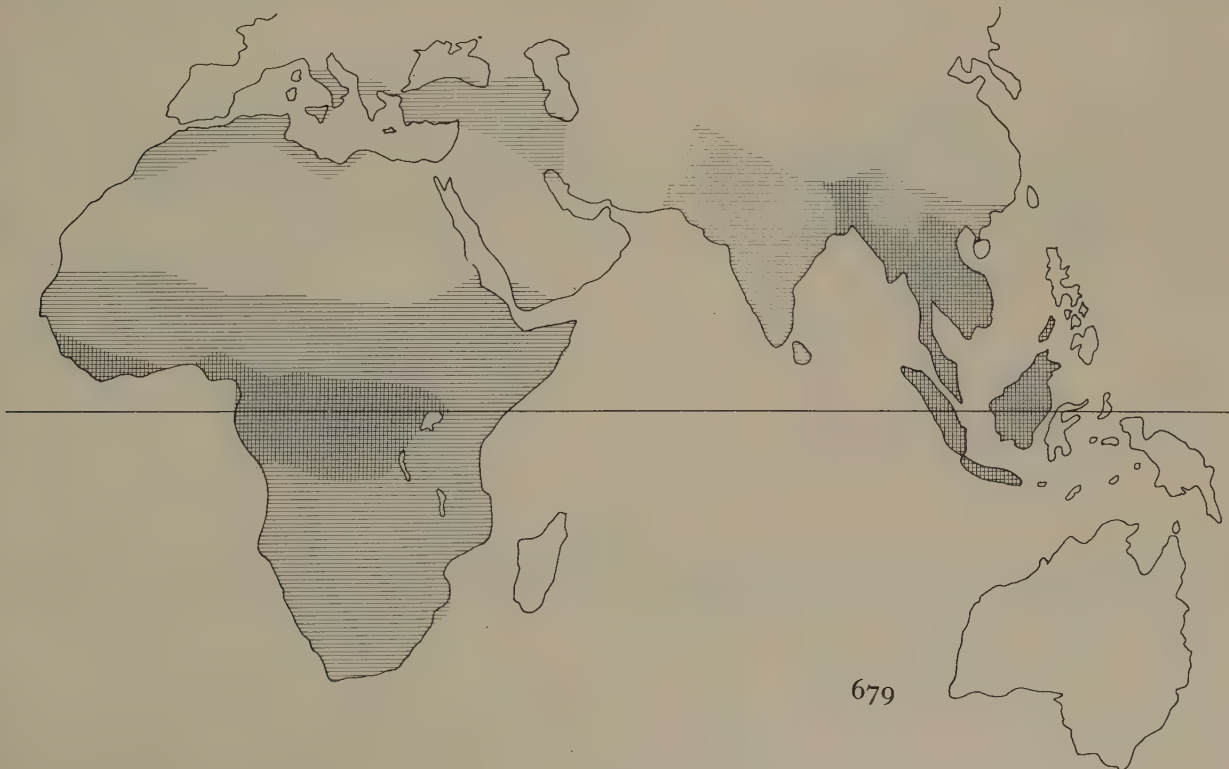
On the Indonesian and Philippine islands there are porcupines that are probably relict forms and these may be taken to represent various stages in the evolution of such an extraordinary and specialized animal as the crested porcupine.

The emigration of forest fauna out into drier habitats is a grand evolutionary spectacle covering a huge time-scale. There can be little doubt that the porcupines have been performers.

The drawings opposite illustrate how the extraordinary structure of the crested porcupine's skull has derived from a generalized typical rodent form, through the progressive inflation of the nasal sinuses.



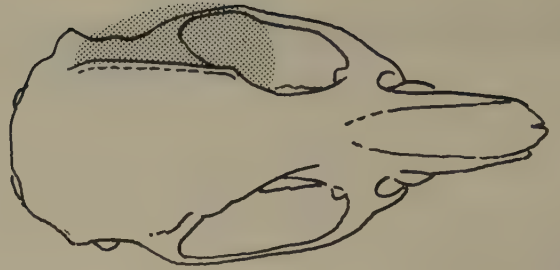
Hystrix upper toothrow.



Old World porcupines: *Atherurinae* (vertical), *Hystriinae* (horizontal).

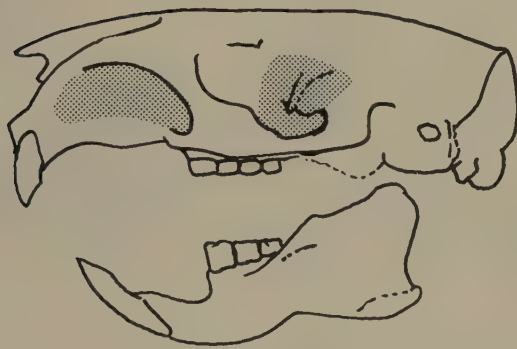


a



b

Dorsal view of the skulls of a *genotypic* Atherurine porcupine, *Atherurus* (a) and a *phenotypic* laboratory rat *Rattus* (b) in which the right temporal muscle has been removed in infancy.

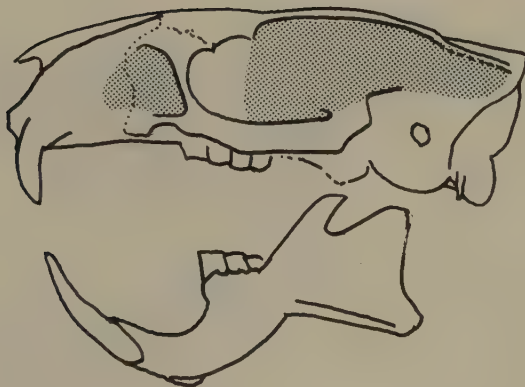


c



d

Lateral view of the skull and mandibles of a *genotypic* *Atherurus* (c) and a *phenotypic* *Rattus* mandible (d) (from right side of skull, b). After Washburn (1947).



e



f

Lateral view of the skulls and mandibles of a *genotypic* Atherurine porcupine *Trichys* (e) and a *genotypic* laboratory rat *Rattus* (f). Stipple: zones occupied by temporalis and masseter (pars anterior). Note strong temporal ridges and angular processes on mandibles.

The enlargement of the porcupine's nasal region has been the cause of much speculation. The most obvious explanation is that the animal has developed an extraordinarily sensitive sense of smell. Corbet and Jones (1965) have suggested instead that it may be an adaptation to a desert habitat "rather comparable to the hypertrophy of the auditory apparatus in groups of desert rodents, allowing sufficient intra and inter-specific communication in a highly dispersed population". Alternatively, for an animal that is most vulnerable on the head, the pneumatic cavities could form a sort of "false hull" surrounding and protecting the brain from injury by taking the first brunt of any unexpected attack.

The skull of *Atherurus* offers an interesting opportunity to correlate form and function in relation to its chewing musculature.

Moore (1965) investigated changes brought about in skull proportions by experimentally varying the activity of the chewing muscles. By feeding rats on an exclusively soft diet he found that their temporalis and masseter muscles were between 9 and 13% lighter than those of rats fed on a hard diet and the angular process was reduced by 4% while an overall decrease in the size of the braincase and facial bones could also be observed. Washburn (1947) and Horowitz and Shapiro (1951) experimentally removed the temporalis muscle in very young rats and noted that the angular process and the temporal ridge failed to develop entirely.

The brush-tailed porcupine has a very poorly developed temporalis muscle and differences can be observed in the skull that parallel those in the rat fed on a soft diet. It appears that this porcupine's masseter; particularly the oblique anterior part has largely taken over the functional role of the temporalis rendering the latter muscle almost as redundant as if it had been cut away: meanwhile the anchorage for the anterior part of the masseter on the maxillary process and on the zygoma are appropriately large. The related porcupine *Trichys* (from South-east Asia) provides a good comparison as this genus has a well-developed temporalis, a long angular process and very marked temporal ridges.

Although the enlarged anterior part of the masseter in *Atherurus* may compensate to some extent for the temporalis, this porcupine certainly has a softer diet than *Hystrix* (and probably *Trichys* as well) feeding mainly on fallen fruit, stems and the roots of swamp forest plants. Like the felid skulls discussed in Vol. I (p. 4) this comparison suggests how physical environment is linked with the adaptive structure of animal form. I hope that the diagrams also hint at how the process of drawing can be an active and useful method for the comparison of forms.



**Brush-tailed
Porcupine**
(*Atherurus africanus*)

Family
Order
Local names

Njiko (Kiswahili), Sekeso (Luganda), Segesse (Kuamba), Kahegenya (Ragoli), Shehekenye (Tereki)

Hystriidae
Rodentia

Measurements
head and body

365—515 mm

tail

155—230 mm

weight

1.5—4 kg (ave. 2—4 kg)

Brush-tailed Porcupine (*Atherurus africanus*)

Races

<i>Atherurus africanus centralis</i>	West Uganda
<i>Atherurus africanus turneri</i>	South Uganda and western Kenya

Brush-tailed porcupines are relatively small animals with peculiar flat gutter hairs over much of their body and a few stout spines on the rump. The genus *Atherurus* is widely distributed in the forested Oriental region and throughout the forest belt of Africa.



The three principal populations of African brush-tailed porcupines have been treated as separate species (Mohr, 1965). The West African *africanus* is distinguished by a swollen frontal region, *centralis* by a shorter toothrow and the East African *turneri* by a shorter and more slender nose. The morphology of porcupine skulls is subject to considerable variation, even within a series from the same locality. In populations that have been subject to several periods of isolation during the past, peculiarities are to be expected, but these populations are still allopatric. Furthermore, Rahm (1962b) who has had the opportunity to study both *centralis* and *africanus* in the field, has stressed that he was unable to see any behavioural or ecological differences between them.



Like the lorises, the chevrotains, the colobines and numerous bat genera, the brush-tailed porcupines seem to be ancient but well adapted forms. In spite of the separation of African and Asian populations (probably since the early Miocene), many common features have been retained.

These animals lead an inconspicuous existence and their range will no doubt be found to be more extensive in East Africa than the present sparse records suggest; the sighting of what might have been a brush-tailed porcupine in the Tana River area adds interest to this extraordinary outpost of forest fauna.

Brush-tailed porcupines are fundamentally forest animals and range from sea level up to 2,300 m in various types of forest. They will even live in quite narrow galleries or riverine strips if there is adequate food and shelter. Rahm has suggested that their habit of living along stream beds is not a sign of semi-aquatic habits but is determined by their need for caves and cavities, which are commonly eroded out of rocks and root ruts in valleys. They are opportunistic where shelters are concerned and may also live in termitaries or burrows dug by other animals. While minor modifications are commonly made, they do not normally dig their own holes. Burrows are used for many years and paths may lead out to established feeding areas. Where a food source appears for a short period, new paths are worn to the supply. Food is eaten on the spot and may occasionally be carried back to the burrow but is never stored.

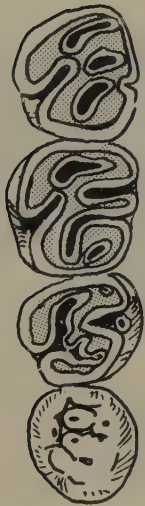


Fallen fruit, roots, tubers and stems are the principal foods. Specially favoured foods are oil palm nuts, *Elaeis*, the fallen seeds of the crabwood tree, *Carapa*, and the fruits of African ginger, *Aframomum*. Other foods listed by Rahm are the fruits of *Pycnanthus*, *Treculia*, *Strombosia*, *Staudtia* and *Uapaca*, the roots of *Ekebergia* and *Rauvolfia* and the leaves and stalks of *Dorstenia*. These porcupines also raid forest-edge cultivation to dig up sweet potatoes and cassava and pick up fallen fruit of both wild and cultivated mango and also paw-paw, guava, banana and avocado pear.

They are capable of some clumsy climbing and can jump well over a metre in height. They also swim well. They are alert and have good hearing, sight and sense of smell. They are playful in captivity and Durrell (1954) describes a slide he found in the Cameroon Forest

"In this cave there was one wall which was a natural slide, a wall of rock some eight feet high sloping to the ground at a gentle angle of 45 degrees. This slide had been worn smooth by the constant passage of the porcupine bodies or bottoms. Judging by the tracks in the sand, they scrambled up to the top of this slope, slid down, walked round, climbed up again and slid down once more. They must have been indulging in this game for a number of generations, as the rock face was worn as smooth as glass".

Brush-tailed porcupines are rather silent except for stamping their feet and rattling the tail, which is furnished with peculiarly specialized quills. Stamping and tail rattling serve as a warning to predators and the silvery-white colour of the tail rattle may also serve to divert attention from the more vulnerable head. The tip of the tail breaks away quite easily. Lang described their protective behaviour



“If irritated, they raise their spines on the posterior half of the body but chiefly of their back. Lowered on their haunches, they rapidly hit one or the other hindfoot on the ground in so rapid a fashion that it is really impossible to see it exactly, thus producing a loud tapping noise. When touched on the back, it makes a rapid movement backwards, but when touched, for instance, on the sides of its neck, it actually throws forward and sideways its posterior portion of the body. This doubling up must be a formidable defence, but in spite of this, I have twice found remains of them in stomachs of leopards, for which they must be an easy prey”. (In Hatt, 1940.)

Some snakes are able to kill and eat these porcupines and one has been found in the stomach of a Gaboon viper, *Bitis gabonica*. However, man and his dogs are the most important enemies.

Rahm found that family groups are formed by a pair with their young. Several “families” sometimes live close together, but each in their own burrow. In this way as many as twenty porcupines may occasionally live in a favoured spot.

The territories of groups of brush-tailed porcupines have been charted by Rahm. He estimated the area to range between 1,800 square metres and five hectares. The territories measured by Rahm were often demarcated by streams and the animals’ dung deposits also might act as territorial markers. Numerous feeding areas are generally enclosed within the territory but, where food is dispersed or seasonally scarce, the porcupines probably have to range over a much wider area. Durrell noticed palm nuts in a porcupine’s burrow, which could only have come from a farm some ten kilometres away. It is just possible that the porcupines had carried them, but it seems more likely that they had been picked up after being carried by birds.

Porcupines are a nuisance in areas where subsistence farmers have cleared forest or in other forest-edge cultivation, but are otherwise harmless. As hosts to a special species of malarial *Plasmodium*, they might be useful for laboratory studies, for they are hardy, easy to keep and fairly prolific. By the same token they could even be domesticated, but could hardly compete with rabbits. They have lived up to fifteen years in captivity.

Their sexual behaviour does not appear to have been described. Gestation is around 100—110 days and up to 3 litters are possible within a year. There is no breeding season.

The chamber in which the young are born is lined with leaves and humus. Between one and four young are born; they are well developed and open their eyes within hours of birth. The quills are soft and the tail is initially scaly with a tuft of fine silver hairs. Rahm, who has only encountered single births, has found that new-born porcupines weigh 150 g. They drink milk for two months and eat solids at two or three weeks. They are very curious and playful and roam about a lot. In captivity, adult males are liable to kill young ones. The porcupine reaches its adult weight at the age of two years.



Porcupines (Hystrix)

Local names

Nungu, Nungunungu (Kiswahili),
 Namunungu (Luganda, Lutoro),
 Ekirungu (Kinyakyusa, Kizanaki),
 Inungu (Gogo), Enyamanungi
 (Lunyoro), Nungwa (Kibende),
 Nunguli (Kinyamwezi, Kibungu),
 Kinyogote (Lukiga, Kiha,
 Runyankole, Runyambo, Kikerewe),
 Ceo coo (Lwo), Ococ (Karamojong,
 Acholi), Icoc (Lango), Echoic
 (Turkana, Itesot), Enjekeche
 (Lugisu), Esegezi (Runyankole),
 Itseketse (Luhya), Kisegese
 (Lusoga), Kischegeshe (Luhaya),
 Nzeghe (Kipare), Nchege (Kikuyu,
 Kimeru), Nzee (Kikamba), Ozuku

(Lugbara, Madi), Sokoso
 (Kimbunga), Sasa (Kirwa, Kitaita),
 Piemsasa (Kichagga), Samti (Iruq),
 Egisabo (Kinatta), Sabutet
 (Kisebei), Sabidit (Masai),
 Chepswererit (Kalenjin), Oyayai
 (Masai), Eyayi (Samburu), Dado
 (Ngulu), Kashito (Somali)

Measurements head and body

600—930 mm

tail

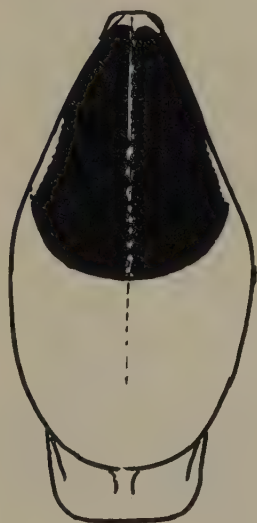
80—170 mm

weight

12—27 kg

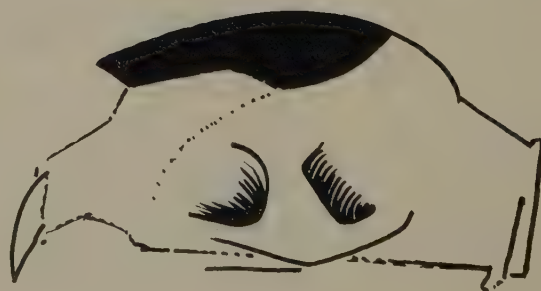
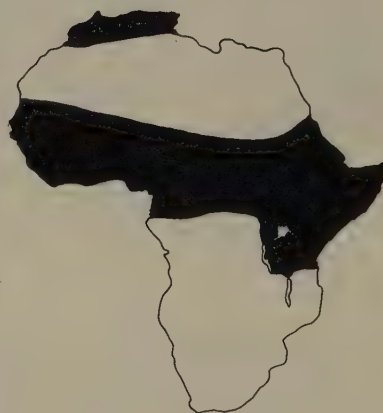
South African Porcupine

Hystrix africae-australis



Crested Porcupine

Hystrix cristata



Porcupines (Hystrix)

The two species of large porcupines found in East Africa are not often differentiated. The most reliable field characteristic by which to tell them apart is the colour of the short rump spines and underside of the tail, which are white in *H. africae-australis* and black or mottled in *H. cristata*. Other distinguishing characteristics require an examination of the animal's tail and skull. The relative development of the nasals and premaxilla and the shape of the rattle quills (reproduced actual size) are illustrated in the visual key opposite.

Species

Hystrix cristata

Hystrix africae-australis



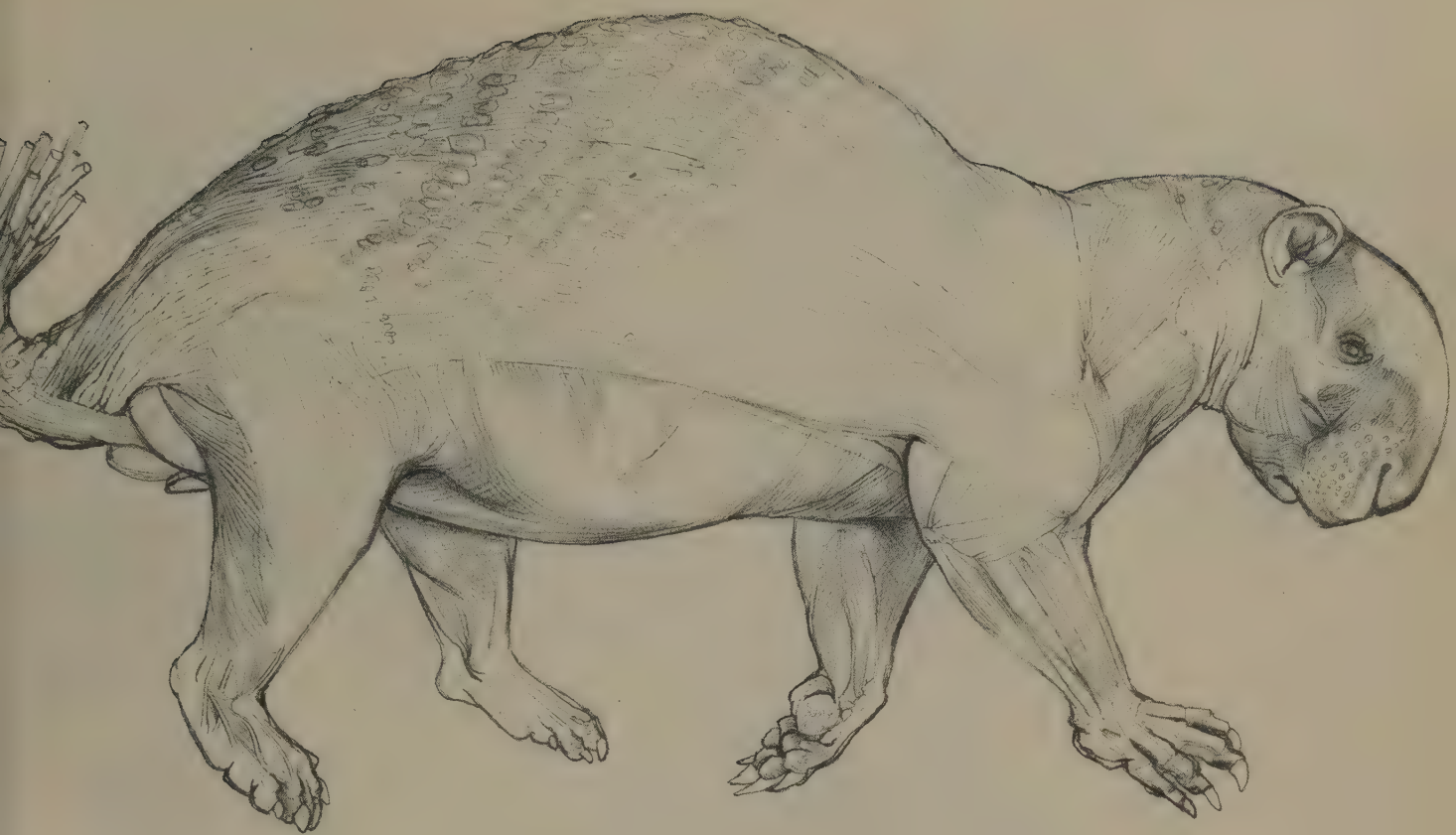
The distribution of porcupines in East Africa is very interesting as the two species are sympatric here. *H. cristata* is a very successful and widespread species, found through a great part of Africa north of the Congo and also in southern Europe, where it might have been introduced by the Romans. It is found in East Africa as far as the Southern Highlands.



Hystrix cristata (juvenile).

H. africae-australis is a southern African species. It appears to be relatively rare in East Africa, but it is a widespread, or even dominant, species in southern areas. *H. africae-australis* has been collected in Ruanda and Kigezi, but also near Kilimanjaro and on Zanzibar Island. These are the most northerly records and all these localities are recognized "Refuge areas". They are also localities well within the range of *H. cristata*. Assuming that the two species originated in Africa as populations that were separated by a tropical forest belt, the much wider range of *H. cristata* and its extension south of the Equator imply a certain superiority for this species. In the broad area of sympatry, extending across the greater part of Tanzania, there are more records of *cristata* than of *africae-australis* and no intermediate forms have been discovered. However, very much more data are needed to explore this interesting situation.

H. cristata have been found in Pleistocene beds in the Sudan, Laetolil and Olduvai. It is not possible with the present very inadequate knowledge of the ecology and behaviour of these porcupines to detect any differences in their habitat or habits, and the following profile is drawn from observations of both



species. As Corbet and Jones (1965) remark:

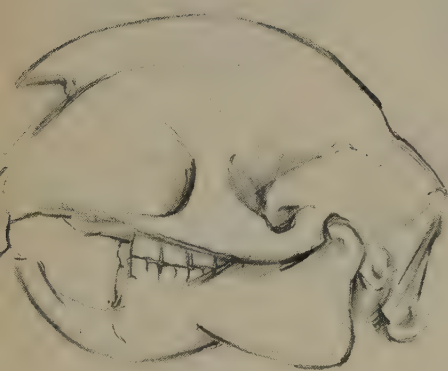
“the consistency of morphological differences strongly suggests some considerable degree of reproductive isolation. . . . The pattern of the rump is probably important for interspecific recognition and it is conceivable that the sound produced by the rattle quills might differ and serve a similar purpose as an ethological barrier”.

Porcupines tend to be commonest in hilly, rocky country but they are adaptable and are extremely widespread in East Africa, occurring in almost all habitats, although they may be absent in the more extensive moist forests and in the most barren desert areas. They are found up to 3,500 m on Kilimanjaro.

Porcupines use or modify natural shelters, caves, crevices amongst the root systems of trees, or holes dug by *Orycteropus*. Where none of these are available, they dig their own burrows, which generally have several entrances or exits, some of them well hidden. They occupy these burrows over many years and in the course of time the passages may become quite extensive. The burrows are frequently littered both within and without by gnawed bones carried there by the porcupines. Apart from the calcium and other minerals gained thereby, these bones may be needed for honing their incisors.

Although carrion is not a common item of diet, they have been seen eating from lion and leopard kills and picking up other dead animals or birds. Roth (1964) reported porcupines carrying impala and warthog heads 750 m back to their burrows in order to nibble the flesh off them.

Their principal foods are roots, barks and fallen fruits. Roots, tubers, rhizomes and bulbs of the following species have been recorded: *Sansevieria*, *Combretum*, *Commiphora*, *Colophospermum*, *Adenia*, *Aloe*, *Ficus petersi*, *Gladioli*, Liliaceae, *Talinum* and *Cyperus*. The fruits of *Kigelia*, *Sclerocarya* and *Strychnos* are among the many fruits eaten. All cultivated root crops are liable to attack from porcupines, particularly cassava, potatoes, carrots, beets and groundnuts which are dug up. If porcupines invade a maize field, they can do a lot of damage in a single night, felling each plant to get at the cobs. They also eat pumpkins and other Cucurbitaceae and can do much damage to young cotton plants. The porcupine has a reputation for being hard to kill and very considerable injuries often heal quickly. The enormously swollen nasal sinuses must help protect vital centres as this outer casing of the skull can be broken without fatal results. When limbs are caught in a trap, they are usually gnawed off and left behind. A juvenile porcupine was found in southern Tanzania with toes missing from both fore and hindlegs on the right side and yet the wounds had already healed perfectly. Brockman (1910) reports a rather grisly incident



“On one occasion, I found two adults and two young porcupines enjoying a siesta under a shady bush close to a large hole. On my disturbing them they made for the hole. I wounded the female, who was the last to enter. As they were near the surface, I endeavoured to drag out the female, who was the nearest, but before I succeeded in getting her out, the male had eaten away nearly the whole of one of her buttocks”.

The porcupines mentioned above had probably been sunbathing, a common habit in nocturnal mammals that live in holes. The porcupine normally emerges after dark and shuffles along, making much noise, grunting and



shaking its quills. At the least encounter with another animal, it raises and fans its quills, which more than doubles its size and makes the black and white quill pattern become even more conspicuous. The visual impact of this display is extraordinarily similar to that of the poisonous scorpion fish, *Pterois volitans*, which wards off many potential enemies by fanning its variegated fin "quills". This display is very easily triggered off in the porcupine and the animal is not particularly discriminating: for instance, one was seen making a great fuss, with all its quills erect, in front of a reedbuck, *Redunca*, on the main road of a Kenya National Park. When the animal is further aggravated, it thumps its feet, whirrs its quills and finally rushes backwards, driving the thicker shorter quills of the rump into its enemy. Lions are not infrequent casualties and also hyaenas (although porcupines and hyaenas live in close association in some places). Leopards are also occasionally wounded but are sometimes successful in killing the porcupine (Cullen, 1969). In the Tanzania Game Department Report for 1953, a black leopard was described as playing with a porcupine. At least one python is known to have died as a result of swallowing a porcupine. Notwithstanding the aggressive effect of its display, the porcupine is a timid animal. Being fond of travelling along tracks or roads, it is often encountered in the headlights of a car, when it usually runs away. The loud noise of the engine may precipitate flight. Wedged in a narrow passage, Sweeney tells of saving himself from an impending facefull of quills by roaring as loudly as he could, whereupon the reversing porcupine ran away (Sweeney, 1966).

The normal gait is a ponderous plantigrade walk, with trotting or galloping resorted to in alarm. They climb very clumsily over rocks and are unable to manage trees; they swim well but probably tire easily. The animal figured here was found drowned in Lake Albert.

Porcupines take readily to captivity and soon become tame and are inmates of many zoos, where individuals have been known to live for as long as 20 years.

Their spoor is very characteristic, as are the elongated pellets which are about 30 mm long.

Family parties such as the one described by Brockman are the commonest social unit and it is unusual for more than seven or eight adults to share a burrow. Apart from the period when the young are being accompanied by one or both parents, adult porcupines forage singly—or perhaps as pairs in the mating season. They like to follow paths and are thought to travel up to 15 km in a night in search of food. During a bush clearance scheme in Uganda, two porcupines were caught in one square mile of savanna.

Porcupine populations like those of other rodents are thought to follow cycles; at least their presence sometimes becomes more conspicuous. Thus the Uganda Game Report of 1938 warned that they were "increasing rapidly" in Bunyoro, and again in the last days of the war (1944–46) many thousands were killed in the same area. They were again common in parts of Uganda in 1953. At such times, porcupines become a serious agricultural pest. They are hunted with dogs and spears or nets after the burrows have been smoked out. They have been exterminated in the heavily settled areas.

Their quills are a favourite ornament and talisman. In Kampala, I have been approached by schoolboys who wanted porcupine quills as a talisman to

ensure they would pass their exams. In the past, quills were also thought to provide a protection against the "enyonyi" syndrome, smallpox and febrile convulsions. Pricking the breast with the quills was thought to relieve mastitis. The hollow rattle quills were widely used in the past as containers for gold dust.

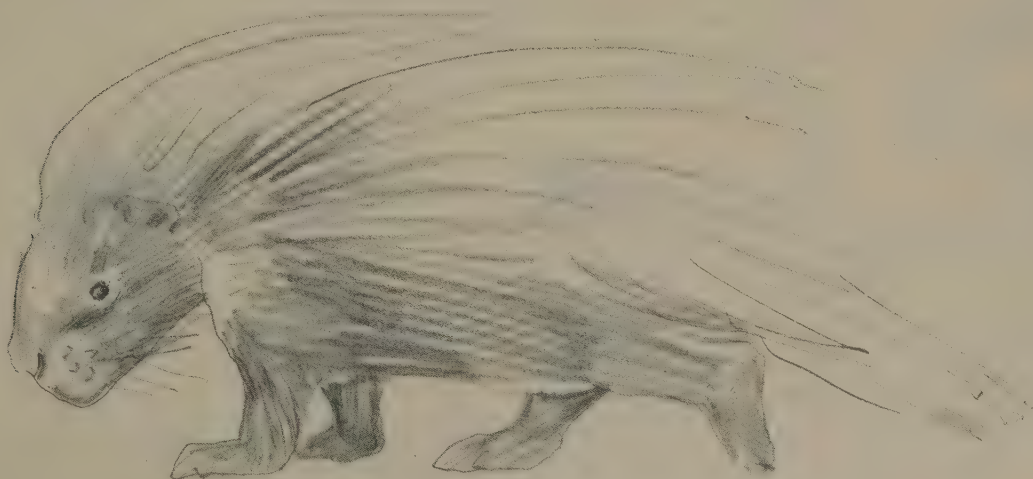
For many years porcupines were used at the Mpwapwa veterinary research station as experimental animals. They are natural hosts of *Glossina* species and provide a potential reservoir for *Trypanosomiasis* (Jordan *et al.*, 1962).

I have seen both sexes of a captive pair shiver their tails before mating. I saw no vocal or other obvious preliminaries but the female raised her tail vertically and flattened her quills before the male's very rapid intromission.

Reports on the gestation period range between 42 and 112 days; eight weeks seems to be the most probable period. They are capable of breeding twice in a year. In southern Africa, *H. africae-australis* breeds during the summer months. In central Africa, Smithers says that they breed between July and December. In East Africa there are few records and it is not known whether they breed once or twice a year, whether they breed seasonally or in what periods of the year.

The young are born in a grass-lined chamber in the burrow, well developed and with their eyes open. At this stage the back quills are present but are rather few and soft. The mother often suckles while squatting; she has 4 or sometimes 6 mammae. In captivity, males have exhibited defensive behaviour, protecting the young between their legs while threatening. The young leave the burrow at the age of one week or more and play by chasing one another.

Roth (1964) weaned a bottle-fed baby porcupine at the age of 6 weeks onto vegetables and fruit, scraps, cereal, herbs and twigs. At about 10 weeks it evinced a preference for animal foods, such as ham and fried meat. The defensive reaction of turning the rump towards disturbance and bristling the quills was present from the start. Although no noise was made by the tiny quills, the baby shivered its tail at any intrusion. It also stamped its back feet while making excited movements, and uttered a series of seven loud grunts. Soft whining squeaks, often repeated, expressed a desire for food or attention. The baby seemed sensitive to cold and seemed to need time to overcome stiffness and sleepiness when it woke up. It showed a remarkable sense of orientation and some memory and soon ranged over an area of about $\frac{1}{2}$ a hectare, knowing all the topography of its home area.



Thryonomyid Rodents

Thryonomyidae

The Thryonomyidae contain the two species of cane rat described in the following profiles. Like the porcupines this hystricomorph rodent has South American counterparts. The resemblances between these rodents may be due to convergence but an ancient common ancestor is also possible.



Thryonomys (Africa).



Carterodon (South America).



Marsh cane-rat
(*Thryonomys swinderianus*)



Savanna cane-rat
(*Thryonomys gregorianus*)

Cane-rats (*Thryonomys*)

The two species of *Thryonomys* occupy distinct ecological niches. One is a semi-aquatic inhabitant of marshes and reed beds; the other is a dry land species of moist savannas. None the less, both species co-exist in parts of central Uganda and in many other areas of East Africa, and their respective habitats are simply higher and lower zones in a local catena. They are therefore widely confused and are seldom recognized as distinct. Incidentally, the names for the cane-rat show how very widespread are the derivatives of the root "ezi" or "enzi".

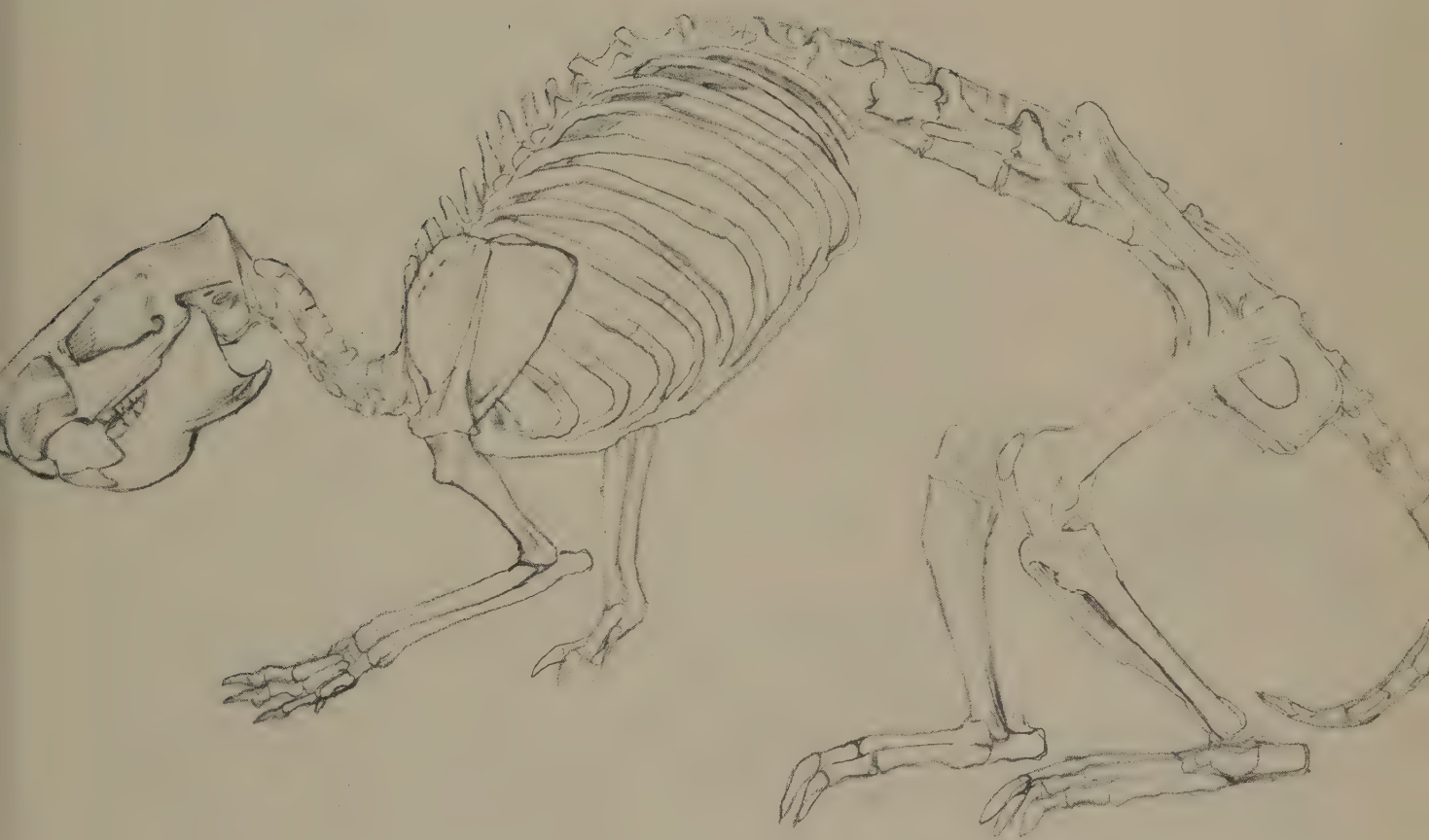
Both species are fundamentally dependent on grass both for cover and food. Both are remarkably successful animals, in spite of being relentlessly persecuted. In many settled areas the principal inducement to firing grass and reeds in the dry season is to hunt out cane-rats. A study of their population dynamics and social behaviour over the year would be of great interest as the number of animals killed each dry season must be considerable.

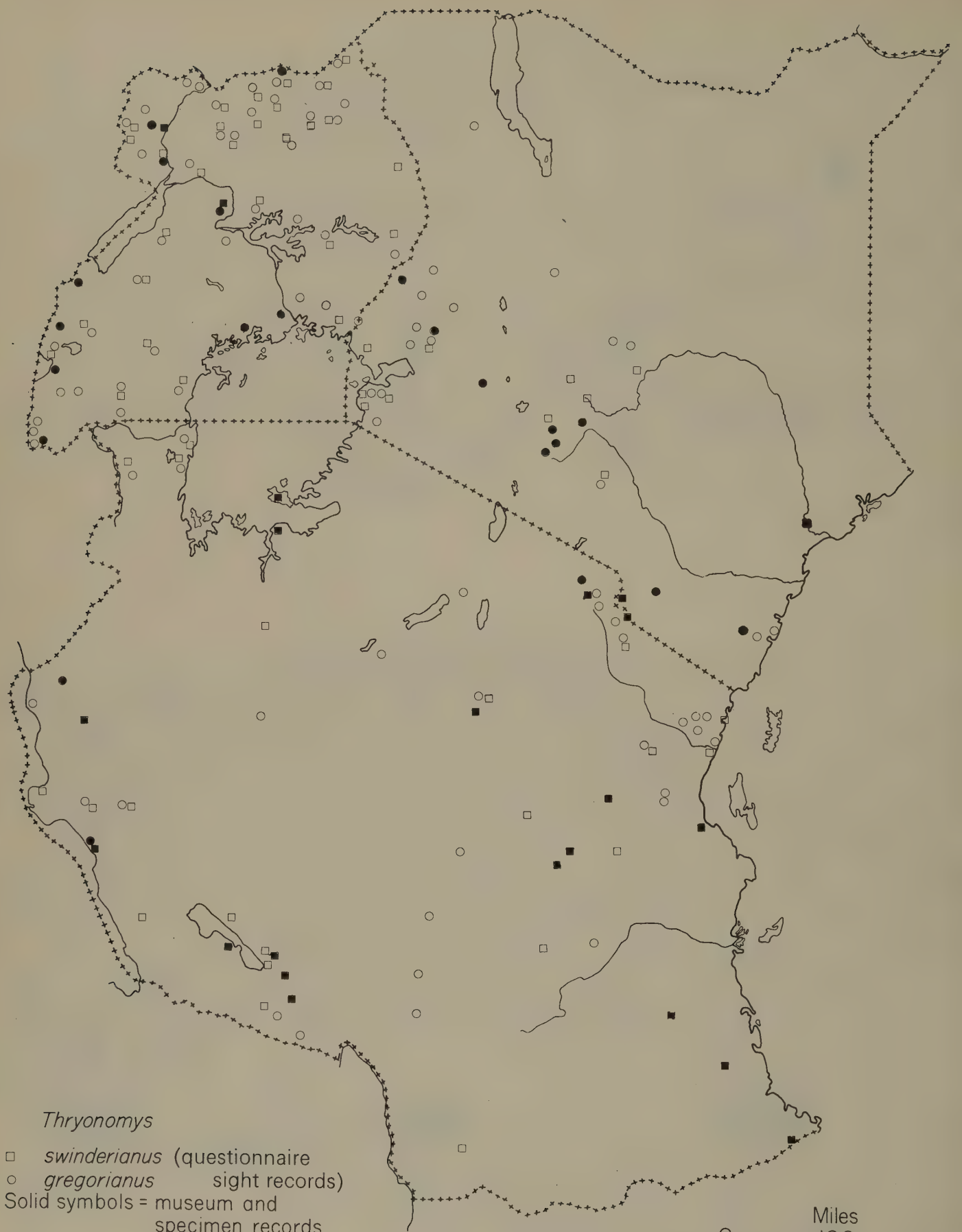


T. swinderianus.



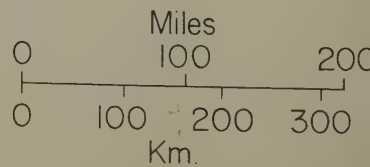
T. gregorianus.





Thryonomys

- *swinderianus* (questionnaire
○ *gregorianus* (sight records)
Solid symbols = museum and
specimen records



Rahm and Christiansen found that *T. gregorianus* live "en famille". *T. swinderianus* also seem to live for part of the year in groups of mixed ages and sexes, but they have been reported to separate during the dry season into larger groups of females, while the males become solitary.

Cane-rats breed at the age of one year and are thought to live not more than three years. In favourable localities between two and six young are born at a time and two litters a year are possible. In view of their potential as a highly acceptable form of protein in Africa, Ajayi (1971) has suggested field management of cane-rats on a sustained yield basis and he has been working on the domestication of *T. swinderianus*. Cane-rats are generally cooked in their skins as the fur is easily plucked out and the soft veal-like flesh disintegrates readily.

Both species gnaw soft rocks, bones and even ivory. This is thought to be more a question of honing their immense chisel-like teeth than a search for mineral supplements.

Cane-rats are surprisingly fast and agile in spite of their tubby appearance. Both species can swim. They hear and smell well and, undoubtedly, depend mainly on these senses for social and sexual communication. Whistles and low hooting grunts have been heard and, like rabbits, they thump their hindlegs when alarmed. That they scarcely use their eyes was demonstrated to me when a savanna cane-rat, walking in short grass, came right up to my foot before taking fright.

During the wet season both species make self-contained corridor systems in the long grass, linking resting places or "forms" with the feeding spots, which are generally on the peripheries of the system.

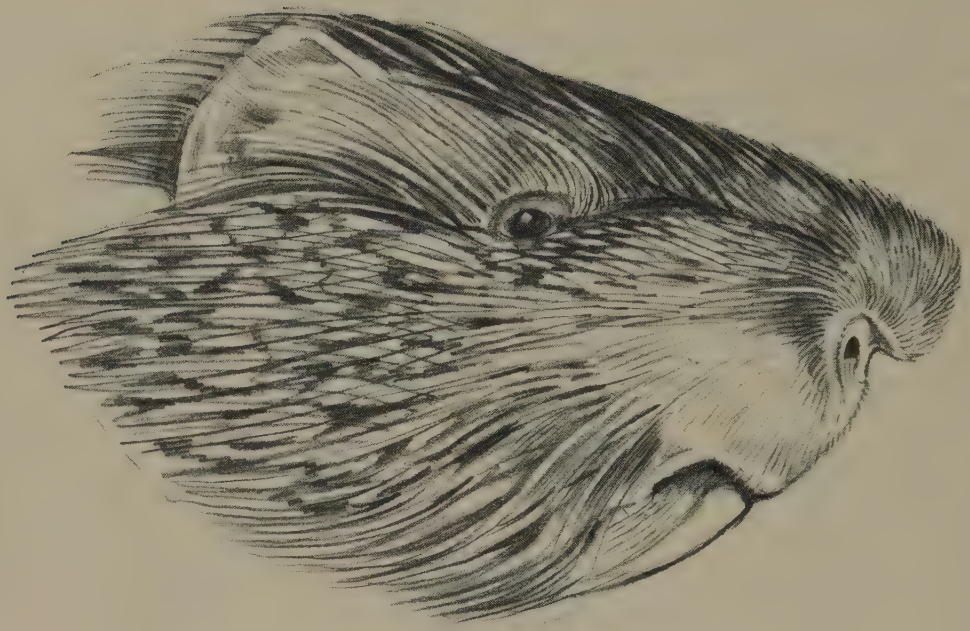
In August–September 1967 the Agriculture Department in Uganda was engaged in converting "bush" into farmland at Kiriandongo near the Victoria Nile. The operation of felling and ploughing up of a square mile of country was attended by over a hundred hunters with dogs and spears. The opportunity was taken to count the animals living in this area, a low-lying *Combretum*, *Terminalia*, *Albizia* savanna, in which the dominant grasses were *Hyparrhenia rufa* on the better drained soils and *Sorghastrum* in the valleys. Both species of cane-rat were present and they were not differentiated in the count. Ninety males, ninety-five females and ten young were caught between August 21 and September 4, giving a figure of about 200 cane-rats to the square mile. Unfortunately the females were not examined for embryos, but the low proportion of young and the even proportion of sexes could suggest that a second mid-rains mating peak was in progress or just over.

Like porcupines and some other rodents, shivering movements of the male's tail have been observed during courtship.

It is not known whether there are differences in the breeding pattern of the two species, but enquiries in northern Uganda suggest that biannual breeding probably takes place in both species, the two seasons being squeezed into the wetter months, March to November. Gestation lasts for about three months and the females suckle the young, standing or lying on their stomach; they have two or three pairs of mammae that are rather laterally placed. The young are born in "forms" or shelters and are well developed at birth; they are soon active and grow fast.



The chin, a target area for social grooming in cane-rats.



**Marsh
Cane-rat**
(*Thryonomys
swinderianus*)

Family Thryonomyidae
Order Rodentia

Local names

Ndezi, Nkungusi (Swahili and many other languages), Nghesi (Kipangwa), Inkezi (Kiha), Ekikezi, Eshenzya (Runyankole), Enkess (Lukiga), Sezi (Kitaita), Esezi (Kibungu), Nsenzi (Kisumbwa, Kinyika, Kimalila), Zenzi (Kibende), Ndehi, Ngungusu (Kingoni), Mirerezi (Kirabai), Mbueresi (Ngulu), Ngenge, Kapenga (Kinyakyusa), Ichengi (Kiambu), Gikeki (Kimeru), Kihehi (Kimatengo), Kihei (Kingindo), Walili (Kikamba), Ndelele (Kiramba), Tehe, Atuya (Acholi), Oyiech, Anyeri (Lwo), Enyuru (Ateso, Karamajong, Turkana), Eshitelele (Isukha, Kisa, Masaba),

Isyavale (Luhia), Esabare (Samia), Esabale-ebunje (Lubukusu), Esabolet (Lugisu), Sabandet (Elgon Masai), Chepkosiret (Kinandi), Kesemgyat (Kalenjin), Burstit (Sebei), Omugongo (*T. swinderianus*), Muswi (*T. gregorianus*) (Lunyoro), Mushwi (Luhaya), Omusu (Luganda, Lusoga, Lukonjo), Alu (Lugbara, Madi), Konu (Kikuyu), Ikudu (Kigweno), Funde (Kirangi), Tukwa (Kizigua), Megore (Masai), Ndoroni (Samburu) Garangw-marwai (Ki-iraqw)

**Measurements
head and body**

432—584 mm

tail

170—262 mm

hindfoot

65—89 mm

weight

4.50—8.80 kg

Marsh Cane-rat

(*Thryonomys swinderianus*)

The marsh cane-rat is generally a somewhat bigger species than *T. gregorianus*, but its most striking differences are its longer tail, very coarse coat and white belly. The coat gives the appearance of being coarser because the individual hairs are shorter. In fact they have the same structure in both species and grow in widely spaced rows, the thick pithy hair having a gutter running along its flattened outer surface. The tail is scaly and its skin is easily shed; indeed the fur, skin and even limbs of cane-rats are very easily torn away.

The marsh cane-rat is much more widely distributed in Africa than the savanna species, extending from Gambia to the southern Sudan and from Kenya to the eastern Cape and southwestern Africa.

This is essentially a semi-aquatic species, living in reed beds and grass areas in valleys and along the margins of rivers and lakes. It may be limited by temperature as it has not been recorded from highland areas, although conditions there often seem suitable on the basis of vegetation alone. Marsh cane-rats make regularly used runways through dense moist vegetation and often take advantage of the shelter of termitary mounds that are generally common in their habitats. They also lie up in shallow depressions that are lined with grass and hidden in dense cover. They favour *Setaria*, *Echinochloa*, *Sorghastrum*, and *Hyparrhenia* grasslands in areas that are waterlogged throughout the wet season. They feed on the roots and shoots of these grasses or canes.* They also eat nuts and fallen fruit and they bark shrubs. They are a pest of sugar cane, maize, millet and cassava growing near their habitat.

They feed sitting on the haunches, after first cutting the base of the food plant and chopping up sections that can be manipulated into the mouth; they eat very rapidly. Cansdale says that they occasionally kill and eat smaller rodents (Rosevear, 1969).

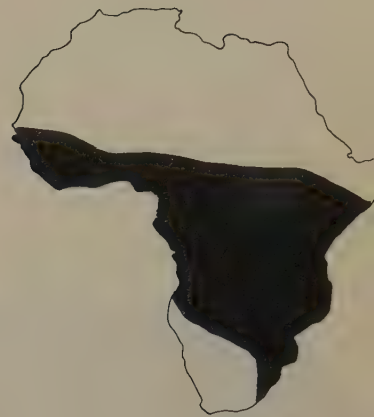
This species is an adept swimmer and an agile runner. They have been kept in captivity and will even breed, but have not lived more than two and a half years, which seems to be a rather short life span for so large an animal. They are more easily heard than seen and their whistling call is a familiar sound in the areas where they live; the thumping of the hindlegs has been mentioned as a habit common to both species of cane-rat.

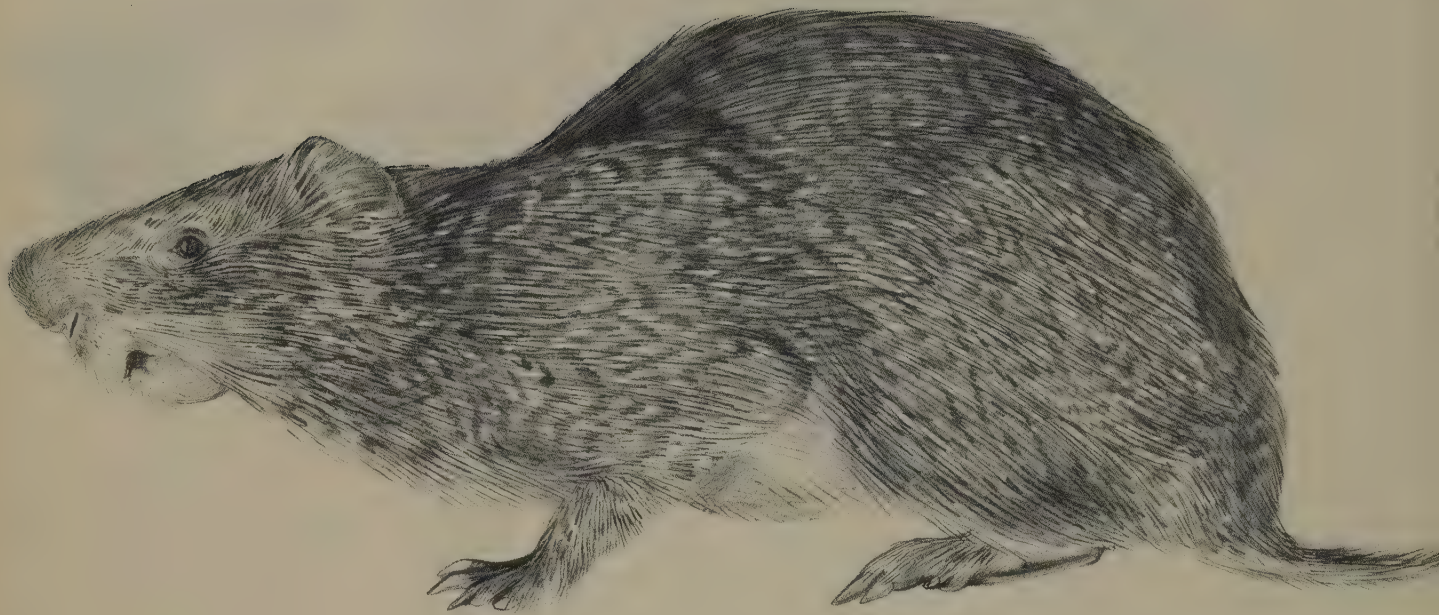
As nothing specific is known of the behaviour of the two species, it is not possible to find and correlate patterns with the slightly different demands of their habitats.

Data on the breeding of cane-rats was presented earlier. In South Africa, young are born from June to August and in West Africa young have been collected from mid-October to January. Ajayi (1971) says that, in Nigeria, *T. swinderianus* has two litters a year.

While they are very small, the young are hidden in their grass-lined nests under a layer of reeds. Four young are usual but as many as six have been recorded. Ajayi found them to be sexually mature at the age of twelve months.

* They are reported to favour the stems of *Echinochloa* in the rains and the roots during the dry season (J. Lokwong, personal communication).





Savanna Cane-rat
(*Thryonomys*
gregorianus)

Family Thryonomyidae
Order Rodentia

Local names

Ndezi, Unkunguzi (Swahili),
Inkezi (Kiha), Enkessi
(Lukiga), Ekikezi (Ruhambo),
Ngenge (Kinyakyusa), Ikengi
(Kiambu), Gikeki (Kimeru),
Isezi (Kibungu), Zenzi (Kibende), Ssenze (Runyankole,
Lukonjo), Eshenzya (Ruhambo), Nsenzi (Kinurka),
Mverezi (Kirabai), Mbuerizi (Ngulu), Ndehi (Kingoni),
Ndelele (Kiramba), Walili (Kikamba), Omusu (Luganda,
Lutoro, Lusoga), Mushwi (Kihehe), Enyuru (Turkana,
Itesot, Karamojong), Anyeri (Lwo), Megore (Kimasai), Alu
(Lugbara), Tukwa (Zigua), Isyavale (Luhia), Esabale,
Esabolet (Lugisu), Kesengyat (Kalenjin), Chepkosiret
(Kinandi), Muriantet (Sebei), Ndoroni (Samburu), Kionu
(Kikuyu).

Measurements
head and body

350—507 mm

tail

65—143 mm (ave. 90)

hindfoot

63—92 mm

weight

2.65—7.5 kg

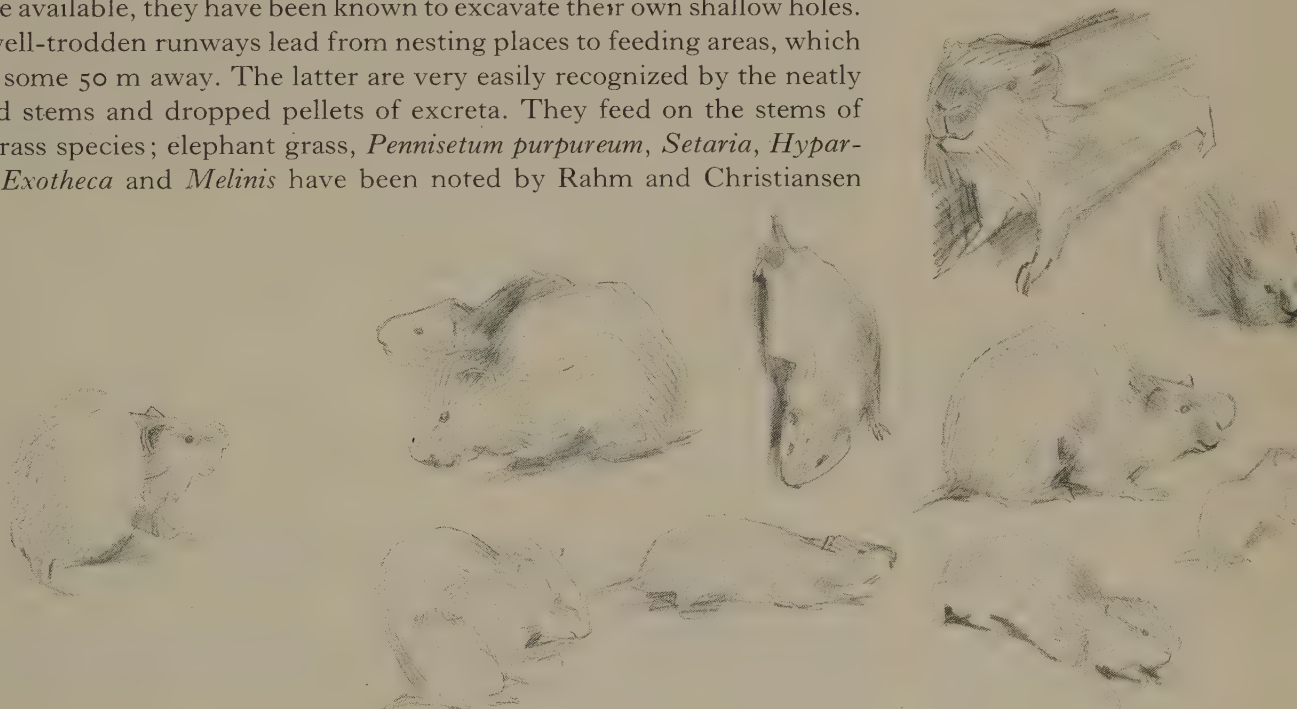
Savanna Cane-rat (*Thryonomys gregorianus*)

The savanna cane-rat does not reach the size or weight of the larger species and the size may be subject to regional variation. The only guide to the identity of cane-rats in the field is the length of the tail. In East Africa the tail of *T. gregorianus* is about 100 mm long, whereas that of an adult *T. swinderianus* is generally more than twice that length. The pattern of grooves on the incisors is the simplest and most reliable key to animals examined in the hand.

The savanna cane-rat is a tropical species, ranging from the northern Cameroons across to the southern Sudan and to the East African coast, and from Mozambique and Malawi to (possibly) the Lower Congo. It tolerates much higher altitudes than the large cane-rat and has been recorded from 2,600 m in the Ruwenzori Mountains.

It is most characteristic of moist savanna and is particularly common in elephant grass, *Pennisetum*, which tends to become dominant in fallow cultivation where there was formerly forest. All over the grassy hills and savannas of Uganda, it is a common and well-known species and also in many moist parts of Kenya and Tanzania.

Well distributed rainfall with the concomitant growth of grass for food and shelter must be a primary need for this species. Long droughts on top of the usual annual hazards of fires and dry season hunting would tend to keep this species scarce or absent in areas of unreliable rainfall (compare the distribution with map in Vol. I, p. 108). While the grass is long and rank, the cane-rats have little need for shelter and they have resting places under grass tufts close to their runways but during the dry season or in rocky areas, they use natural shelters, crevices, termitaries and *Orycteropus* holes. When none of these are available, they have been known to excavate their own shallow holes. Their well-trodden runways lead from nesting places to feeding areas, which may be some 50 m away. The latter are very easily recognized by the neatly chopped stems and dropped pellets of excreta. They feed on the stems of many grass species; elephant grass, *Pennisetum purpureum*, *Setaria*, *Hyparrhenia*, *Exothea* and *Melinis* have been noted by Rahm and Christiansen





(1963). Bracken, *Pteridium*, is an important food in montane areas and wild ginger, *Aframomum*, in well wooded and wet areas. They also bark certain trees and shrubs and pick up nuts and fruit. They raid cultivation to dig up groundnuts or sweet potatoes and they also fell cassava and maize plants for their stems as well as eating pumpkins.

Although primarily nocturnal, they are sometimes encountered in daylight, particularly during the rains when there is a lot of cover, shade and moisture.

The typical social unit, a small party or family group, is estimated to occupy a territory of 3,000—4,000 sq. m (Rahm and Christiansen). This territorial area was measured at a time of the year when conditions were at their best and can give little indication of the overall ecological needs of a population, even in ideal conditions. Likewise the population turnover and fluctuations in numbers must be immense. Their predators include man-servals, leopards and other large cats, pythons, viverrids and various birds of prey. Chapin (1932) reported migratory eagles, *Aquila nipalensis* arriving at Uelle in time to feed on the cane-rats, when the annual fires drove them into the open.

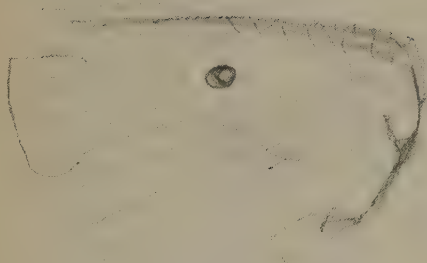
The data on breeding are remarkably scarce. A baby was collected in southern Kenya on December 10 and a pregnant female was recorded for November and another for December (Hollister, 1919). In northern Uganda they are reported to be seasonal breeders bearing their young at the end of the dry season in February and March.

Studying penned *Thryonomys*, Ewer (1968) found a male fought other males but lived amicably with two females and their young. The latter were growled at occasionally but if they wagged the tail they were not molested.

Ritualized fighting consists of a snout-to-snout pushing contest with sudden rotations of the head. These may be followed by a lightning sideways flip of the rump to knock the opponent off balance. Inferiors not fleeing fast enough may be bitten but only in the rump. The victor was seen to scratch the ground, drag its anal glands and rub its cheeks after fighting.

Mutual grooming of the head and chin is common within established groups. Courtship is initiated by the male tail wagging and treading the hind legs. Eventually the pair rear up and touch noses. Copulation follows further treading and grooming by the male.

Grass stems are felled by the young at an early age but stripping of seeds by pulling the stem through the mouth has to be learnt. The young have playful pushing contests.



Thryonomys swinderianus. Note shape of nasal area adapted for use as a buffer in pushing contests.

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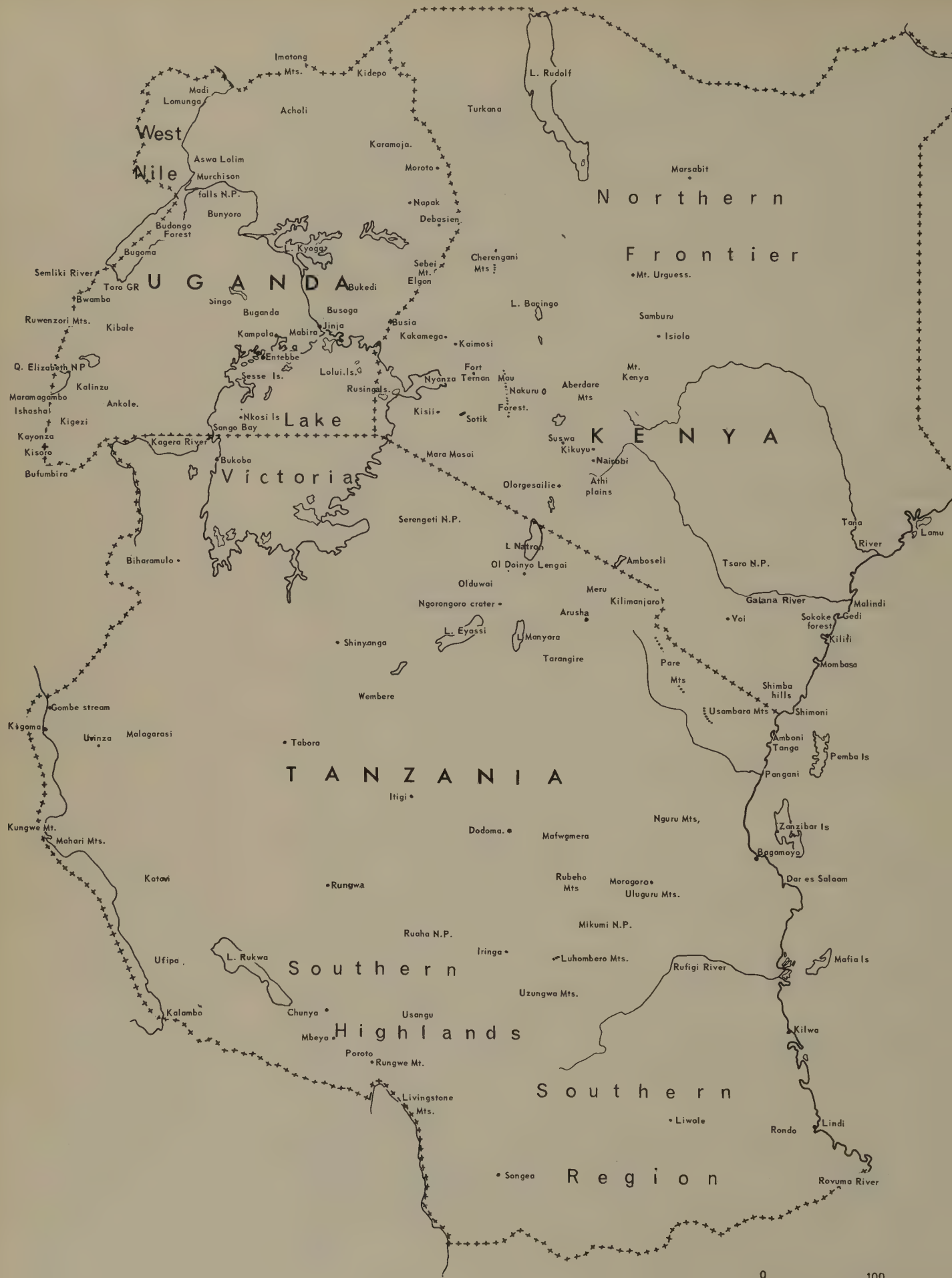
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Gazetteer



Abercorn Zambia $8^{\circ} 50' S$ $31^{\circ} 25' E$
 Aberdare Mts C. Kenya $1^{\circ} 20' - 1^{\circ} 40' N$ $36^{\circ} 40' E$
 Acholi N. Uganda
 Albert, Lake W. Uganda
 Amboni N.E. Tanzania $5^{\circ} 3' S$ $39^{\circ} 4' E$
 Amboseli S. Kenya $2^{\circ} 40' S$ $37^{\circ} 10' E$
 Angola S.W. Africa
 Ankasa Forest, Ghana
 Ankole S. Uganda
 Arusha N. Tanzania $3^{\circ} 23' S$ $36^{\circ} 43' E$
 Aswa-Lolim G.R. $2^{\circ} 35' N$ $31^{\circ} 45' E$
 Athi Plains C. Kenya $1^{\circ} 30' S$ $36^{\circ} 50' E$
 Avakubi Zaire $1^{\circ} 30' N$ $27^{\circ} 25' E$
 Bagamoyo Tanzania Coast $6^{\circ} 25' S$ $38^{\circ} 54' E$
 Baringo Lake $0^{\circ} 40' N$ $36^{\circ} 5' E$
 Biafra W. Africa
 Biharamulo N.W. Tanzania $2^{\circ} 38' S$ $31^{\circ} 19' E$
 Botswana Southern Africa
 Budongo W. Uganda $1^{\circ} 45' N$ $31^{\circ} 40' E$
 Bufumbira Mts E. Congo W. Uganda
 Buganda S. Uganda
 Bugoma W. Uganda $1^{\circ} 20' N$ $31^{\circ} E$
 Bukedi E. Uganda $0^{\circ} 40' N$ $33^{\circ} 50' E$
 Bukoba N.W. Tanzania $1^{\circ} 21' S$ $31^{\circ} 48' E$
 Bunyoro W. Uganda
 Burundi C. Africa
 Busia E. Uganda $0^{\circ} 30' N$ $34^{\circ} 8' E$
 Busingiro (see Budongo) W. Uganda
 Busoga S.E. Uganda
 Bwamba W. Uganda $0^{\circ} 40' N$ $30^{\circ} E$
 Cameroons W. Africa
 Central African Republic or Congo Brazzaville

Central Refuge E. Congo (Zaire)
 Chad Lake W. Africa
 Chania River, Mt Kenya, Chandlers Falls N.F.D. Kenya 1° N $37^{\circ} 45'$ E
 Cherengani Mts W. Kenya $1^{\circ} 15'$ N $35^{\circ} 25'$ E
 Chitau Angola
 Chunya S.W. Tanzania $8^{\circ} 32'$ S $33^{\circ} 25'$ E
 Comoros Islands Indian Ocean E. of Madagascar
 Congo basin C. Africa
 Congo River C. Africa
 Cross River Nigeria
 Dabaga C. Tanzania $8^{\circ} 7'$ S $35^{\circ} 55'$ E
 Dar-es-Salaam Tanzania Coast $6^{\circ} 48'$ S $39^{\circ} 18'$ E
 Darfur W. Sudan
 Debasien, Mt E. Uganda $1^{\circ} 45'$ N $34^{\circ} 50'$ E
 Dodoma C. Tanzania $6^{\circ} 11'$ S $35^{\circ} 45'$ E
 Dungilia River Southern slopes of Ruwenzori
 Dura River W. Uganda $0^{\circ} 30'$ N $30^{\circ} 25'$ E
 Echuya Swamp S.W. Uganda $1^{\circ} 15'$ S $29^{\circ} 45'$ E
 Edward Lake W. Uganda
 Elgon, Mt E. Africa $1^{\circ} 10'$ N $34^{\circ} 35'$ E
 El Obeid Sudan
 Embu C. Kenya $1^{\circ} 30'$ S $37^{\circ} 30'$ E
 Eritrea Red Sea Coast
 Ethiopia N.E. Africa
 Ethiopian Faunal Region African Continent with Arabia
 Eyassi, Lake C. Tanzania $3^{\circ} 40'$ S 35° E
 Fayum Egypt
 Fernando Po Is W. Africa
 Fort Ternan W. Kenya $0^{\circ} 20'$ S $35^{\circ} 25'$ E
 Gabon, Gaboon W. Africa
 Gambia W. Africa
 Garguess or Urguess, Mt (now known as Warges N.F.D. Kenya)
 Garissa N.F.D. Kenya $1^{\circ} 30'$ N $39^{\circ} 40'$ E
 Gedi Kenya Coast $3^{\circ} 18'$ S 40° E
 Ghats "African Ghats" E. Tanzania
 Gombe Stream Reserve W. Tanzania $4^{\circ} 59'$ S $30^{\circ} 57'$ E
 Greek River S.E. Uganda $1^{\circ} 28'$ N $34^{\circ} 35'$ E
 Gregory Rift Eastern Rift Valley, Kenya
 Hannington, Lake Kenya $0^{\circ} 20'$ N $36^{\circ} 5'$ E
 Haut Ituri N.E. Zaire 2° N $30^{\circ} 30'$ E
 Hoggar or Ahaggar Mts Algerian Sahara
 Horn of Africa N.E. Africa
 Imatong Mts S. Sudan 4° N $32^{\circ} 50'$ E
 Impenetrable Forest (now Bwindi) S.W. Uganda $1^{\circ} 5'$ S $29^{\circ} 40'$ E
 Iringa S. Tanzania $7^{\circ} 47'$ S $35^{\circ} 42'$ E
 Ishasha W. Uganda $0^{\circ} 48'$ S $29^{\circ} 35'$ E
 Isiolo G.R. $0^{\circ} 22'$ N $37^{\circ} 35'$ E
 Itigi Thicket C. Tanzania $5^{\circ} 40'$ S $34^{\circ} 30'$ E
 Ituri E. Congo

Ituri Maniema E. Congo (Zaire)
 Ivory Coast West Africa
 Jinja S. Uganda $0^{\circ} 25' N 33^{\circ} 15' E$
 Jombeni Mts C. Kenya $0^{\circ} 25' N 38^{\circ} E$
 Kabale W. Uganda $1^{\circ} 18' S 30^{\circ} E$
 Kadam, Mt E. Uganda $1^{\circ} 45' N 34^{\circ} 40' E$
 Kagera River Uganda, Tanzania border
 Kaimosi W. Kenya $0^{\circ} 18' N 34^{\circ} 55' E$
 Kaiso W. Uganda $1^{\circ} 35' N 30^{\circ} 58' E$
 Kakamega W. Kenya $0^{\circ} 20' N 34^{\circ} 45' E$
 Kalahari S.W. Africa
 Kalinzu W. Uganda $0^{\circ} 30' S 30^{\circ} E$
 Kampala S. Uganda $0^{\circ} 20' N 32^{\circ} 35' E$
 Kanjera Kenya $0^{\circ} 55' S 36^{\circ} 25' E$
 Karagwe N.W. Tanzania $1^{\circ} 15' S 31^{\circ} 50' E$
 Karamoja E. Uganda
 Kasai River Congo basin
 Kashasha River Kivu District, Zaire
 Katanga Southern Zaire
 Katavi Plain W. Tanzania $6^{\circ} 30' - 7' S 31^{\circ} E$
 Kayonza W. Uganda $1^{\circ} S 29^{\circ} 35' E$
 Kenya Highlands C. Kenya
 Kenya, Mt E. Africa $0^{\circ} 10' S 37^{\circ} 25' E$
 Kiambu C. Kenya $1^{\circ} 10' S 36^{\circ} 15' E$
 Kibale Forest W. Uganda $0^{\circ} 30' N 30^{\circ} 35' E$
 Kidepo Valley N. Uganda $3^{\circ} 50' N 33^{\circ} 55' E$
 Kigezi W. Uganda $1^{\circ} S 30^{\circ} E$
 Kigogo S.W. Tanzania $8^{\circ} 37' S 35^{\circ} 15' E$
 Kigoma W. Tanzania $4^{\circ} 52' S 29^{\circ} 38' E$
 Kikuyu C. Kenya $1^{\circ} 20' S 36^{\circ} 40' E$
 Kilifi Kenya Coast $3^{\circ} 40' S 39^{\circ} 50' E$
 Kilimanjaro N. Tanzania $3^{\circ} S 38^{\circ} E$
 Kilombero River and Valley Tanzania $9^{\circ} S 36^{\circ} E$ to $8^{\circ} S 37^{\circ} E$
 Kilwa Tanzania Coast $8^{\circ} 45' S 39^{\circ} 25' E$
 Kinshasha Congo Kinshasha
 Kiriandongo N.W. Uganda $1^{\circ} 50' N 32^{\circ} 7' E$
 Kiserawe Dar-es-Salaam $6^{\circ} 53' S 39^{\circ} 3' E$
 Kisoro W. Uganda $1^{\circ} 18' S 29^{\circ} 40' E$
 Kisii W. Kenya $0^{\circ} 40' S 34^{\circ} 45' E$
 Kivu, Lake E. Congo
 Kivu Province E. Congo
 Kungwe, Mt W. Tanzania $6^{\circ} 8' S 20^{\circ} 48' E$
 Kyarumba Ruwenzori $0^{\circ} 10' N 29^{\circ} 55' E$
 Kyoga, Lake C. Uganda $1^{\circ} - 2^{\circ} N 33^{\circ} E$
 Laetolil near Olduvai N. Tanzania
 Lamia River, Bwamba Uganda
 Lamu Kenya Coast $2^{\circ} 20' S 40^{\circ} 58' E$
 Liberia W. Africa (Limpopo Rivers borders N. Transvaal S. Africa)
 Lindi Tanzania Coast $10^{\circ} S 39^{\circ} 45' E$

Livingstone Mts S.W. Tanzania
 Liwale S.E. Tanzania $9^{\circ} 47' S 37^{\circ} 58' E$
 Loita Plains C. Kenya $1^{\circ} S 35^{\circ} 35' E$
 Lolokwi, Mt N.D.F. Kenya $1^{\circ} 20' N 37^{\circ} 17' E$
 Lolui Is. Lake Victoria $0^{\circ} 10' S 33^{\circ} 45' E$
 Lomunga G.R. $3^{\circ} 35' N 31^{\circ} 30' E$
 Luhombero, Mt C. Tanzania
 Lushoto N. Tanzania $4^{\circ} 47' S 38^{\circ} 17' E$
 Mabira S. Uganda $0^{\circ} 30' N 32^{\circ} 50' E$
 Madehani S.W. Tanzania $9^{\circ} 20' S 34^{\circ} E$
 Madi N.W. Uganda
 Mafia Is. Tanzania Coast
 Mafuga Forest Plantation S.W. Uganda $1^{\circ} 10' S 29^{\circ} 45' E$
 Mahari Mts W. Tanzania $6^{\circ} S 30^{\circ} E$
 Makerere, Kampala S. Uganda
 Malagarasi W. Tanzania $4^{\circ} 5' S 29^{\circ} 30' E$
 Malawi C. Africa (also Lake Malawi)
 Malindi Kenya Coast $3^{\circ} 8' S 40^{\circ} 10' E$
 Manyara, Lake N. Tanzania $3^{\circ} 30' S 35^{\circ} 50' E$
 Mara Masai G.R. S.E. Kenya
 Maramagambo W. Uganda $0^{\circ} 30' S 29^{\circ} 50' E$
 Marsabit N. Kenya $2^{\circ} 25' N 38' E$
 Masaka S.W. Uganda $0^{\circ} 20' S 31^{\circ} 40' E$
 Masindi W. Uganda $1^{\circ} 45' N 31^{\circ} 40' E$
 Matanga N. Pemba Is.
 Matengo Hills $11^{\circ} S 34^{\circ} 50' E$
 Matopos Hills Rhodesia
 Mau Forest Kenya $35^{\circ} 35' S 36^{\circ} 20' E$
 Mauritania Western Sahara
 Mawokota S. Uganda $0^{\circ} 22' N 32^{\circ} 22' E$
 Mayanja Forest near Kampala
 Mbale East Uganda $1^{\circ} 5' N 34^{\circ} 10' E$
 Mbeya S.W. Tanzania $8^{\circ} 54' S 33^{\circ} 26' E$
 Menengai, Mt $0^{\circ} 10' S 36^{\circ} 5' E$
 Meru, Mt Tanzania $3^{\circ} 15' S 36^{\circ} 45' E$
 Mgogoni N. Pemba Is.
 Mikumi Nat. Park E. Tanzania
 Milanje, Mt S. Malawi
 Mkulumuzi Caves N.E. Tanzania $5^{\circ} 3' S 39^{\circ} 4' E$
 Mombasa Kenya Coast $4^{\circ} S 39^{\circ} 35' E$
 Momella, Lakes N. Tanzania $3^{\circ} 12' S 36^{\circ} 52' E$
 Mongiro Bwamba Uganda
 Morogoro E. Tanzania $6^{\circ} 48' S 37^{\circ} 40' E$
 Moroto E. Uganda $2^{\circ} 30' N 34^{\circ} 45' E$
 Mozambique E. Africa
 Moyale N.F.D. Kenya $3^{\circ} 30' N 35^{\circ} 5' E$
 Moyovosi River N.W. Tanzania
 Mpwapwa C. Tanzania $6^{\circ} 22' S 36^{\circ} 30' E$
 Muheza Usambra Mts N. Tanzania

Muko Forest Plantation S.W. Uganda $1^{\circ} 12' S 29^{\circ} 50' E$
 Murchison Falls Nat. Park (now Kabalega) W. Uganda $2^{\circ} 20' N 31^{\circ} 40' E$
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 Nakuru C. Kenya $0^{\circ} 20' S 36^{\circ} 5' E$
 Namalusi Is., Port Bell Uganda $0^{\circ} 19' N 32^{\circ} 36' E$
 Namaqualand S.W. Africa
 Namuli, Mt Mozambique
 Napak E. Uganda $2^{\circ} 8' N 20^{\circ} 34' E$
 Natal S. Africa
 Ngorongoro Crater N. Tanzania $3^{\circ} 10' S 35^{\circ} 35' E$
 Ngurdoto Crater $3^{\circ} 13' S 36^{\circ} 52' E$
 Nguru Mts E. Tanzania $60^{\circ} S 37^{\circ} 30' E$
 Nigeria W. Africa
 Nimba Mt Guinea and Liberia
 Nkata Bay Malawi
 Northern Frontier District (N.F.D.) Kenya
 Nyanza S.W. Kenya
 Nyasa, Lake (Lake Malawi) Central S.E. Africa
 Nyika Plateau N. Malawi
 Nyiro, Mt Kenya $0^{\circ} 47' N 47^{\circ} E$
 Nuba Mts Sudan
 Okavango Swamp S.W. Africa
 Oldonyo Lengai, Mt $2^{\circ} 46' S 35^{\circ} 55' E$
 Olduvai Gorge N. Tanzania $3^{\circ} S 35^{\circ} 20' E$
 Olorgesailie S. Kenya $1^{\circ} 40' S 36^{\circ} 28' E$
 Omo S. Ethiopia $5^{\circ} N 36^{\circ} E$
 Oubangui River, marks northern border of Zaire
 Pangani River Tanzania Coast $5^{\circ} 26' S 38^{\circ} 58' E$
 Pare Mts N. Tanzania
 Pemba Is. $4^{\circ} 50' - 5^{\circ} 30' S 39^{\circ} 45' E$
 Poroto Mts S.W. Tanzania $9^{\circ} S 34^{\circ} E$
 Queen Elizabeth Nat. Park (now Ruwenzori N.P.) W. Uganda
 Rondo Plateau S. Tanzania $10^{\circ} 10' S 39^{\circ} 10' E$
 Rovuma River S. Tanzania $10^{\circ} 45' S 33^{\circ} 40' E 10^{\circ} S 48^{\circ} E$
 Ruaha Park C. Tanzania
 Ruaha River System Central and S.E. Tanzania
 Ruanda (now Rwanda C. Africa)
 Rubeho Mts E. Tanzania
 Rudolf, Lake N. Kenya
 Rufigi River E. Tanzania $8^{\circ} 31' S 37^{\circ} 22' E 8^{\circ} S 39^{\circ} 25' E$
 Rukwa, Lake S.W. Tanzania $7^{\circ} 35' - 8^{\circ} 32' S 31^{\circ} 48' - 35^{\circ} 52' E$
 Rungwe, Mt S. Tanzania $9^{\circ} 8' S 33^{\circ} 40' E$
 Rusinga Is. Kenya $0^{\circ} 25' S 34^{\circ} 18' E$
 Ruwenzori Mts W. Uganda
 Sango Bay S. Uganda $0^{\circ} 55' S 31^{\circ} 45' E$
 Sankuru River Congo basin
 Songwe Caves S.W. Tanzania $8^{\circ} 50' S 33^{\circ} 8' E$

Salisbury, Lake E. Uganda $1^{\circ} 35' N 34^{\circ} 15' E$
 Sebei E. Uganda $1^{\circ} 20' N 34^{\circ} 35' E$
 Selinda, Mt E. Rhodesia
 Semliki Forest Reserve W. Uganda $0^{\circ} 4' N 30^{\circ} E$
 Semliki River W. Uganda and E. Congo $1^{\circ} N 30^{\circ} 20' E$
 Senegal W. Africa
 Serengeti Nat. Park N. Tanzania
 Serengeti Plains N. Tanzania $2^{\circ} 25' - 3^{\circ} 5' S 34^{\circ} 40' - 35^{\circ} 20' E$
 Sesse Is. N. Lake Victoria
 Shimba Hills $4^{\circ} 20' S 39^{\circ} 35' E$
 Shimoni S. Kenya Coast $4^{\circ} 45' S 39^{\circ} 25' E$
 Shinyanga C. Tanzania $3^{\circ} 33' S 33^{\circ} 25' E$
 Sierra Leone W. Africa
 Singo county C. Uganda
 Sipi E. Uganda $1^{\circ} 25' N 34^{\circ} 25' E$
 Sokoke Forest $3^{\circ} 15' S 39^{\circ} 55' E$
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 Sotik W. Kenya $0^{\circ} 40' S 35^{\circ} 38' E$
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 Tana River E. Kenya $0^{\circ} - 2^{\circ} 50' S 38^{\circ} - 40^{\circ} 30' E$
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 Tiwi Kenya Coast $4^{\circ} 10' S 39^{\circ} 35' E$
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 Transvaal S. Africa
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 Turkwell River flowing into S. Lake Rudolf
 Uelle N.E. Congo (Zaire)
 Ufipa S.W. Tanzania $7^{\circ} - 8^{\circ} S 31^{\circ} 30' E$
 Ugalla River N.W. Tanzania
 Ukerewe Is. Lake Victoria $2^{\circ} S 33^{\circ} E$
 Uluguru Mts E. Tanzania $6^{\circ} 51' S 37^{\circ} 44' E$
 Upper Guinea W. Africa
 Urguess, Mt or Garguess or Warges N. Kenya $0^{\circ} 58' N 37^{\circ} 28' E$
 Usambara Mts N.E. Tanzania $5^{\circ} 6' S 38^{\circ} 38' E$
 Usangu or Buhoro Flats S.W. Tanzania $8^{\circ} 30' S 34^{\circ} 5' E$

Uvinza W. Tanzania $5^{\circ} 7' S 30^{\circ} 22' E$
 Uzungwa Mts C. Tanzania $7^{\circ} 45' - 8^{\circ} 35' S 45^{\circ} - 36^{\circ} 12' E$
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 Virunga Volcanoes W. Uganda and E. Congo $1^{\circ} 30' S 29^{\circ} 35' E$
 Voi E. Kenya $3^{\circ} 28' S 38^{\circ} 35' E$
 Wami River E. Tanzania $6^{\circ} 30' S 37^{\circ} E - 6^{\circ} S 39^{\circ} E$
 Wembere Depression C. Tanzania $3^{\circ} 45' - 5^{\circ} 10' S 33^{\circ} 40' - 34^{\circ} 45' E$
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 Zambia C. Africa
 Zanzibar Is. $5^{\circ} 43' - 6^{\circ} 28' S 39^{\circ} 11' - 39^{\circ} 41' E$
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